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Leucaena cultivars – current releases and future opportunities
Cultivares de leucaena – estado actual y oportunidades futuras

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Abstract

The *Leucaena* genus is made up of 24 different species (19 diploid and 5 tetraploid species). However, early use of the *Leucaena* genus in agricultural systems was based entirely upon a very narrow germplasm base. A single genotype of *Leucaena leucocephala* ssp. *leucocephala* ('common' leucaena) was spread pantropically from its center of origin in Mexico over 400 years ago. Genetic improvement of *Leucaena leucocephala* began in the 1950s, when vigorous 'giant' leucaena (*L. leucocephala* ssp. *glabrata*) was identified in Australia and Hawaii. Cultivars such as Hawaiian Giant K8, Peru and El Salvador were selected and promoted for grazing in Australia and multipurpose agroforestry uses throughout the tropics. Plant breeding for improved forage production resulted in the release of cv. Cunningham in 1976 in Australia. These cultivars of 'giant' *Leucaena leucocephala* displayed broad environmental adaptability, with the exception of poor tolerance of cold temperatures (and frost) and acid soils. The outbreak of the psyllid insect pest (*Heteropsylla cubana*) from Cuba during the 1980s devastated both 'common' and 'giant' leucaena all around the world. This challenge resulted in renewed interest in lesser-known *Leucaena* spp. that exhibited tolerance to the pest and in interspecific hybridization as a means of developing new cultivars. Some 'giant' leucaena lines exhibited excellent agronomic traits and a degree of tolerance to the psyllid pest and this resulted in the release of new cultivars in Australia (cvv. Tarramba and Wondergraze) and Hawaii (cv. LxL). Since the 1990s, plant breeding programs have sought to develop cultivars with greater psyllid tolerance using interspecific hybridization. This has resulted in the release of cv. 'KX2-Hawaii' for timber and forage production, and a backcrossed forage cultivar cv. Redlands (Australia). Both cultivars are based upon interspecific hybridization between *L. pallida* and *L. leucocephala* ssp. *glabrata*. Cold-temperature and acid-soil tolerance have been pursued in South American breeding programs based upon *L. diversifolia*, without commercial success. The development of sterile *Leucaena* spp. cultivars is currently underway to nullify the environmental weed potential of all current commercial cultivars. Tolerance to cold temperatures (*L. diversifolia*, *L. pallida*, *L. pulverulenta* and *L. trichandra*), frost (*L. greggii* and *L. retusa*) and psyllids (*L. collinsii*) exists within the *Leucaena* genus and may be exploited in future hybridization programs. New genetic analyses and molecular plant breeding techniques have the potential to facilitate further gene transfer between *Leucaena* spp. for the development of the next generation of multipurpose cultivars.

Keywords: Hybridization, plant breeding, psyllid resistance, tree legumes.

Resumen

El género *Leucaena* está compuesto por 24 especies diferentes (19 diploides y 5 tetraploides). Sin embargo, en su primera fase el uso del género *Leucaena* en sistemas agropecuarios se basó exclusivamente en una estrecha base de germoplasma. Un solo genotipo de *Leucaena leucocephala* ssp. *leucocephala* (leucaena 'común') fue el que que hace más de 400 años se dispersó pantropicalmente desde su centro de origen en México. El mejoramiento genético de *Leucaena leucocephala* comenzó en la década de 1950, cuando se identificó una vigorosa leucaena 'gigante' en Australia y Hawái, *L. leucocephala* ssp. *glabrata*. Cultivares como Hawaiian Giant K8, Peru y El Salvador fueron seleccionados y promovidos para pastoreo en Australia y usos agroforestales múltiples en todo el trópico. Un programa de fitomejoramiento buscando mayor rendimiento de forraje resultó en la liberación del cv. Cunningham en 1976 en

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Australia. Los cultivares del tipo 'gigante' de *Leucaena leucocephala* mostraron una amplia adaptabilidad a las condiciones ambientales, con excepción de tolerancia a temperaturas bajas (incluyendo heladas) y suelos ácidos. El brote del insecto plaga *Heteropsylla cubana* (Psyllidae) durante la década de 1980 tuvo un efecto devastador en las leucaenas 'común' y 'gigante' en todo el mundo. Este desafío dio lugar a un renovado interés en especies menos conocidas de *Leucaena* que mostraran tolerancia a la plaga, y en la hibridación interespecífica como medio para desarrollar nuevos cultivares. Algunas líneas de leucaena 'gigante' exhibieron excelentes características agronómicas y cierta tolerancia a la plaga de los psílidos, lo que dio lugar a la liberación de nuevos cultivares en Australia (cvv. Tarramba y Wondergraze) y Hawái (cv. LxL). Desde la década de 1990, programas de fitomejoramiento han buscado desarrollar cultivares con mayor tolerancia a los Psyllidae utilizando la hibridación interespecífica. Como resultado se liberó el cv. 'KX2-Hawaii' para la producción de madera y forraje, y cv. Redlands en Australia, un cultivar forrajero retrocruzado. Ambos cultivares están basados en la hibridación interespecífica entre *L. pallida* y *L. leucocephala* ssp. *glabrata*. En Sudamérica se llevaron a cabo proyectos de mejoramiento basados en *L. diversifolia* buscando tolerancia a temperaturas bajas y suelos ácidos, sin embargo sin éxito comercial. Proyectos actualmente en curso tienen como objetivo desarrollar cultivares de *Leucaena* spp. estériles para eliminar el potencial de maleza ambiental de los actuales cultivares comerciales. Dentro del género *Leucaena* sí existen características como tolerancia a temperaturas bajas (*L. diversifolia*, *L. pallida*, *L. pulverulenta* y *L. trichandra*), a heladas (*L. greggii* y *L. retusa*) y a los psílidos (*L. collinsii*) y se podrán explotar en futuros programas de hibridación. Las nuevas técnicas disponibles de análisis genético y reproducción molecular de plantas tienen el potencial de facilitar la transferencia de genes entre especies de *Leucaena* con el fin de desarrollar la próxima generación de cultivares multipropósito.

Palabras clave: Fitomejoramiento, *Heteropsylla cubana*, hibridación, leguminosas arbóreas, resistencia a plagas.

History

Utilization of multipurpose trees from the 24 species of the *Leucaena* genus (Abair et al. 2019) has been occurring for millenia in subsistence agricultural systems in seasonally dry forest areas throughout their native range extending from southern Texas, USA to northern Peru (Hughes 1998). In the 16th century, Spanish colonists in Central America recognized the potential of leucaena as an animal forage and began the spread of 'common' weedy leucaena (*L. leucocephala* ssp. *leucocephala*) throughout the tropics (Gray 1968; Brewbaker 2016). 'Common' leucaena is a small branchy tree with low biomass yield, poor form, early flowering and heavy seed production (Gray 1968). This remarkable plant has wide adaptability to a range of soil types and climatic conditions, where it has become established in disturbed environments (Campbell et al. 2019; Idol 2019). 'Common' leucaena has been utilized by subsistence smallholder farmers pantropically to produce fuelwood, timber, green manure, shade, animal forage and human food. It has also been trialled for use in commercial agriculture as a fodder for ruminant animals (Takahashi and Ripperton 1949; Kinch and Ripperton 1962).

During the 1950s agronomists and plant breeders in Australia and Hawaii began programs to identify and develop superior leucaena cultivars for adoption in commercial agricultural systems (Gray 1968; Brewbaker 2016). Seed of 'common' leucaena was collected from disparate areas and evaluated. It soon became apparent that 'common' leucaena lacked diversity in key agronomic characteristics (Gray 1968), indicating that this phenotype was genetically identical all around the world, having originated from a narrow genetic base. This was later confirmed by molecular genetic analysis (Sun 1992).

Advances in genetic improvement followed the identification and commercialization of 'giant' types of leucaena (*L. leucocephala* ssp. *glabrata*) in Hawaii (Hawaiian Giant K8 – 1975, K28, K29, K67 and K72; Brewbaker et al. 1972) and Australia (El Salvador – 1962, Peru – 1962, Tarramba – 1997; Gray 1968; Oram 1990). The 'giant' types had superior vigor/yield and less precocious seed production (Hutton and Gray 1959; Brewbaker et al. 1972; Brewbaker 1975). Tree form varied within the 'giant' types, with some accessions being arboreal (Hawaiian Giant K8, El Salvador and Tarramba), while others had a greater degree of basal branching (Peru). These early cultivars of 'giant' leucaena have been widely distributed around the world for use in tropical agroforestry systems. A comprehensive, authoritative review of the history of genetic improvement of the *Leucaena* genus has been compiled by Professor J.L. Brewbaker, University of Hawaii (UH) (Brewbaker 2016).

Plant breeding programs have combined the superior attributes of different accessions of 'giant' leucaena, with breeding objectives including: increased forage yield and branched tree form suitable for direct grazing; and more recently, tolerance of the psyllid insect.

Cultivar Cunningham (public domain cultivar in Australia) is an intraspecific hybrid based upon cv. Peru and was released as a forage type by the Commonwealth Scientific and Industrial Research Organisation (CSIRO) within Australia in 1976 (Oram 1990). It was selected for superior forage yield and branched form (Hutton and Beattie 1976). Cunningham has been widely planted in Australia and around the world.

The emergence of a devastating pantropical psyllid insect pest (*Heteropsylla cubana*) during 1983–1990 (Bray 1994), triggered a second phase of genetic evaluation and cultivar development. A number of accessions of 'giant' leucaena had moderate tolerance to the psyllid. These formed the basis of the following cultivars:

- cv. LxL: A synthetic line of 6 intraspecific hybrid forage breeding lines released by the University of Hawaii (UH) in 1996 (Austin et al. 1998). Despite having superior forage yield (~15% heterosis), cv. LxL has had limited commercial utilization in the USA (Brewbaker 2016).
- cv. Tarramba (protected by PBR in Australia): A bred line (UH) from accession K636 collected from highlands in Coahuila, Mexico (Brewbaker 2016) and released in Australia in 1997 (Anonymous 1997). Key attributes of cv. Tarramba are: erect arboreal habit; excellent biomass and forage production; some cool-temperature tolerance; moderate tolerance of the psyllid insect pest; and reduced seed production. Cultivar Tarramba has been readily adopted in smallholder ruminant feeding systems in Indonesia (Kana Hau and Nulik 2019), where its erect stems are valued for fuelwood and construction timber.
- cv. Wondergraze (protected by PBR in Australia): Selfed progeny (S4) from an intraspecific cross between accession K584 and cv. Tarramba bred by UH and released in Australia in 2010 (Anonymous 2008). Key attributes of cv. Wondergraze are: moderate tolerance of the psyllid insect pest; good forage yield; branched tree form; and excellent seedling vigor.

Environmental limitations to 'giant' leucaena

The following environmental constraints restrict the productivity of 'giant' leucaena: defoliation by frost; poor growth under cool temperatures; and lack of tolerance of acid soils (Hutton 1983). While 'giant' leucaena can survive severe frost by regrowing from the root crown during spring (Felker et al. 1998), minor frost (0 to -3 °C) burns the leaves from plants and moderate frost (<-3 °C) kills stems to ground level (Dalzell et al. 1998a; Middleton and Clem 1998;). This restricts the ability of farmers in subtropical areas to utilize 'giant' leucaena forage during the winter protein feed gap, when it would be of tremendous benefit to livestock production. Growth of 'giant' leucaena slows significantly when average daily temperatures drop below 25 °C and average monthly minimum temperatures drop below 22 °C (Mullen et al. 2003c), restricting forage production during spring and autumn in subtropical areas and year-round production in the elevated tropics. 'Giant' leucaena thrives on neutral-alkaline calcareous soils. It grows poorly on acid soils (pH water 1:5 <5.2) due to calcium and phosphorus deficiency and aluminum toxicity adversely impacting root growth, rhizobium nodulation and nitrogen fixation (Hutton 1983). There are large tracts of acid soils in tropical areas that would otherwise be suitable for 'giant' leucaena development.

Interspecific hybridization

Many of the lesser-known *Leucaena* spp. have agronomic traits that address the limitations to adaptation of *L. leucocephala* ssp. *glabrata*, including: psyllid resistance (*L. collinsii*, *L. esculenta* and *L. pallida*) (Mullen et al. 2003b); cold tolerance (*L. diversifolia*, *L. pallida* and *L. trichandra*) (Mullen et al. 2003c); and frost tolerance (*L. greggii*, *L. pulverulenta* and *L. retusa*) (Hughes 1998). However, these species cannot be commercialized directly in agroforestry systems because they have other serious limitations to utility such as low biomass/forage yield (*L. greggii* and *L. retusa*) (Mullen et al. 2003a), poor forage quality (*L. diversifolia*, *L. esculenta*, *L. greggii*, *L. pallida*, *L. pulverulenta* and *L. trichandra*) (Dalzell et al. 1998b; Jones et al. 1998) and potentially a lack of longevity or tolerance of regular defoliation (*L. esculenta*, *L. greggii*, *L. pallida* and *L. retusa*) (Mullen et al. 2003a).

A high degree of interspecific cross compatibility has been identified within the *Leucaena* genus (Gonzalez et al. 1967; Sorensson and Brewbaker 1994). Interspecific hybridization enables plant breeders to combine superior traits from different species to form the basis of populations for further selection and genetic improvement. Hybridization programs have been undertaken to develop new cultivars of *Leucaena* with the following characteristics:

Low mimosine forage

Variability in concentration of the toxic amino acid mimosine in foliage exists within the *Leucaena* genus. Species with lower concentrations of mimosine include: *L. pulverulenta* (Gonzalez et al. 1967; Brewbaker et al.

1972; Bray et al. 1984); and *L. collinsii*, *L. diversifolia*, *L. shannonii* and *L. trichandra* (Brewbaker and Kaye 1981; Saunders et al. 1987). Hybridization to produce low-mimosine forage cultivars for feeding to monogastric animals has been attempted. Hybrid lines of *L. pulverulenta* × *L. leucocephala* ssp. *glabrata* were developed with low mimosine concentration in Australia; however, the programs were unsuccessful as low-mimosine breeding lines (~25% reduction in mimosine) had significantly lower forage yields than existing commercial cultivars (Bray et al. 1984).

Acid soil tolerance

In general, little specific tolerance to acid soils was identified within the *Leucaena* genus by a comprehensive environmental adaptation study (Mullen et al. 2003c). However, acid soil tolerance has been reported within accessions of *L. diversifolia* and *L. trichandra* (Hutton 1983). Hybrid breeding programs (× *L. leucocephala* ssp. *glabrata*) in South America (CIAT/EMBRAPA) and Southeast Asia (MARDI) have been undertaken to develop psyllid-tolerant and acid soil-tolerant forage cultivars (Wong et al. 1998). Two hybrid cultivars were released in Malaysia in 1998 (Aminah and Wong 2004), cv. Bharu (*L. trichandra* × *L. leucocephala* ssp. *glabrata* breeding line 40-1-18) and cv. Rendang (*L. diversifolia* × *L. leucocephala* ssp. *glabrata* breeding line 62-6-8). The commercial success of these cultivars is unknown and wider assessment of their agronomic performance and forage quality (palatability and digestibility) is required. Concentrations of condensed tannins in both cultivars have been reported to be high and to adversely impact rumen function (Khamseekhiew et al. 2000; Kok et al. 2013; Saminathan et al. 2015, 2017). These hybrid cultivars need to be compared with alternative multipurpose shrub legumes with known acid soil tolerance, e.g. *Calliandra calothyrsus*, *Cratylia argentea* and *Flemingia macrophylla*.

Psyllid resistance

Hybrid cultivars have been developed from *L. pallida* × *L. leucocephala* ssp. *glabrata* (designated KX2 hybrids) for forage and biomass/timber. These hybrids have shown high yield with broad environmental adaptation (Mullen et al. 2003c), psyllid resistance (Mullen et al. 2003b), cool tolerance (Austin et al. 1997; Mullen et al. 2003c) and intermediate forage quality (Dalzell et al. 1998b).

- Cultivar KX2-Hawaii was bred by UH and was released in 2007 (Brewbaker 2008). This cultivar was developed by 6 cycles of recurrent selection from advanced generations of the original F1 hybrid *L. pallida* K376 × *L. leucocephala* ssp. *glabrata* K8. It was selected under regular cutting/coppicing for psyllid resistance, forage/biomass yield and self-sterility. To date, there has been limited commercial utilization of cv. KX2-Hawaii.
- Cultivar Redlands (protected by PBR in Australia) was bred by the University of Queensland (Anonymous 2015) and was released in 2017. This hybrid cultivar was developed using 5 elite KX2 F1 hybrids bred by UH. These parents were open-pollinated (panmixia) and F2 seed planted for intense selection (5–10% retention) under the criteria of psyllid resistance, yield, tree form (high degree of basal branching) and self-sterility. After another cycle of recurrent mass selection, elite F3 trees were backcrossed (BC) (hand-pollinated) to *L. leucocephala* ssp. *glabrata* cv. Wondergraze. Elite psyllid-resistant BC progeny were backcrossed again to produce breeding lines that were effectively 87.5% cv. Wondergraze and 12.5% *L. pallida*. The best BC2 breeding lines were then self-pollinated 3 times. Selfed breeding lines were assessed for in vitro forage quality (digestibility plus crude protein and condensed tannin concentrations) and their palatability determined under direct grazing. Cattle had a preference for cvv. Cunningham and Wondergraze plots ahead of cv. Redlands, but cv. Redlands was readily eaten (Shelton et al. 2019). A trial comparing hedgerow pastures of cvv. Wondergraze and Redlands and measuring cattle liveweight gain is currently underway in north Queensland (Lemin et al. 2019). Cultivar Redlands is recommended for humid (average annual rainfall >800 mm) psyllid-prone areas.

Cold tolerance

Hybrids based upon *L. diversifolia* (KX3) and *L. pallida* (KX2) with *L. leucocephala* ssp. *glabrata* have been developed by UH and distributed for evaluation throughout the tropics (Brewbaker 2016). These hybrids are vigorous, psyllid-resistant/tolerant and have superior growth under cool temperatures during autumn and spring in the subtropics (Middleton and Clem 1998; Mullen et al. 2003a, 2003c) and year-round in the elevated tropics (Austin et al. 1997). The forage quality of these hybrids requires careful evaluation, as it is likely to be lower than 'giant' leucaena owing to higher concentrations of condensed tannins inherited from *L. diversifolia* and *L. pallida* (Austin et al. 1997; Dalzell et al. 1998b). With the exception of cv. KX2-Hawaii, no cultivars from this breeding program have been commercialized. KX3 hybrids have been developed and evaluated in southern

Brazil (Austin et al. 1998) and Argentina (Goldfarb and Casco 1998) for frost and cold tolerance; however, no known commercial cultivars have been released from these programs.

Wood/biomass/pulp production

Fast-growing *Leucaena* spp. hybrids have great potential for high-value timber, biomass (bioenergy) and paper pulp production (Brewbaker 2016). Cultivar KX4-Hawaii is a male-sterile triploid hybrid between *L. leucocephala* ssp. *glabrata* K636 and *L. esculenta* K838 developed by UH (Brewbaker 2013). This hybrid is vegetatively propagated, psyllid-tolerant, arboreal, vigorous and cool-tolerant. Significant areas (>18,000 ha) of 'giant' leucaena in Gujarat, Maharashtra and Madhya States in India are managed for wood production to supply paper pulp mills (Khanna et al. 2019). Genetic improvement of 'giant' leucaena germplasm has been undertaken through intense selection and mutagenesis to improve biomass yield. A triploid *L. collinsii* × *L. leucocephala* ssp. *glabrata* hybrid has been developed by JK Paper Ltd (Khanna et al. 2019) and is currently being vegetatively propagated for evaluation of biomass yield and paper pulp characteristics. This hybrid also has potential as a forage plant and requires wider evaluation for environmental adaptation, forage production and animal feeding.

Sterility

'Common' and 'giant' leucaena have the potential to become environmental weeds of disturbed ruderal habitats in the absence of grazing animals (Campbell et al. 2019; Idol 2019). Breeding programs within Australia are currently developing sterile cultivars for use in extensive grazing systems in jurisdictions where the promotion of 'giant' leucaena is not sanctioned. Strategies are focussing on developing sterility (male or female) in commercial cultivars via mutagenesis (McMillan et al. 2019) or gene editing to prevent flowering (Real et al. 2019). Interspecific hybridization to develop sterile triploids is also being explored (Real et al. 2019). In addition to reducing or eliminating the weed potential of *Leucaena* spp. cultivars, sterility may confer a significant yield (forage or biomass) advantage as plant resources are not diverted from vegetative growth to seed production.

Future directions for cultivar development

Superior accessions of lesser-known *Leucaena* spp. (Table 1) have been identified in extensive germplasm evaluation trials (Mullen et al. 2003a; 2003b; 2003c). These could be utilized to develop new interspecific hybrids to overcome the lack of cold, frost and acid soil tolerance in current commercial cultivars. Other accessions within these lesser-known taxa are held within international germplasm collections and require further agronomic evaluation (consult the World Leucaena Catalogue; Bray et al. 1997).

As understanding of the genetic base of the *Leucaena* genus improves, new tools have become available for plant breeding. Phylogenetic studies of the evolutionary history of the *Leucaena* genus have identified the parents of the 5 allotetraploid species (Govindarajulu et al. 2011a) and enabled the definition and elucidation of relationships between the 19 diploid species (Govindarajulu et al. 2011b; Abair et al. 2019). Sequencing of the *L. trichandra* genome has been completed and will enable genetic markers to be identified for traits of interest in breeding programs (Abair et al. 2019). Application of molecular marker-assisted selection should accelerate rates of genetic gain in traditional and molecular plant breeding programs.

Chromosome/ploidy doubling has been successfully undertaken in a number of *Leucaena* spp. (Shi 2003). Diploid species could be doubled, which may enhance cross-compatibility for desired interspecific hybrids. *Leucaena collinsii* (2n) is of particular interest as a forage plant as it is psyllid-resistant (Mullen et al. 2003b), has moderate forage yield (Mullen et al. 2003a; 2003c), excellent in vitro forage quality (Dalzell et al. 1998b) and has proved productive under cattle grazing (Jones et al. 1998). Producing and evaluating artificial tetraploid *L. collinsii* lines could deliver valuable new forage cultivars. Similarly, halving ploidy levels of the tetraploid *Leucaena* spp. would generate diploid (2n) lines that could be used to develop sterile triploid cultivars. Gametophytic self-incompatibility systems could be used to produce F1 interspecific hybrid seed (Brewbaker 2016).

New genetic technologies have potential to modify the *Leucaena* genome, including transgenic improvement, e.g. suppressing mimosine synthesis by the transfer of a gene from *Rhizobium* sp. into *L. leucocephala* ssp. *glabrata* K636 via agrobacterium (Jube and Borthakur 2010), or gene deletion using CRISPR technology (Real et al. 2019). Mutagenesis has been used to alter the genome of *L. leucocephala* ssp. *glabrata* to increase plant yield (Khanna et al. 2019) or induce sterility (McMillan et al. 2019).

Modern vegetative propagation techniques can be used for embryo rescue of F1 interspecific hybrid seeds that are prone to abort and to mass produce elite sterile germplasm for commercial application.

Table 1. Superior accessions of key *Leucaena* spp. for use in future hybridization programs [adapted from Mullen et al. (2003a; 2003b; 2003c)].

Breeding objective	Constraint	Taxon	Accession
Forage	Cold tolerance	*L. diversifolia*	K778, K784, K806, OFI104/94, CPI33820
		L. pallida	K748, K802, K376, CQ3439
		L. trichandra	OFI53/88, OFI35/88
	Frost tolerance	*L. retusa*	-[1]
	Sterility (2n parent)	*L. collinsii*	OFI51/88, OFI52/88
		L. magnifica	OFI1984, OFI58/88
Timber/biomass/ paper pulp/shade	Cold tolerance	*L. diversifolia*	K778, K784, K806, OFI104/94, CPI33820
		L. pallida	K748, K802, K376, CQ3439
		L. trichandra	OFI53/88, OFI35/88
	Frost tolerance	*L. pulverulenta*	-[1]
		L. greggii	-[1]
		L. retusa	-[1]
	Sterility (2n parent)	*L. cruziana*	OFI51/87
		L. esculenta	-[1]
		L. magnifica	OFI1984, OFI58/88
		L. macrophylla ssp. *istmensis*	OFI47/85
		L. macrophylla ssp. *macrophylla*	OFI55/88
		L. multicapitula	OFI81/87
		L. pulverulenta	-[1]
		L. salvadorensis	-[1]
		L. trichandra	OFI53/88, OFI35/88

[1]Superior accessions not identified – evaluation of a diverse array of accessions required.

Challenges and opportunities for future cultivar development

Many of the lesser-known *Leucaena* taxa have been identified only within the last 30 years and are represented by few accessions/provenances, e.g. *L. confertiflora*, *L. cuspidata*, *L. involucrata*, *L. lempirana*, *L. magnifica*, *L. matudae* and *L. pueblana*, from limited geographical areas in international germplasm collections (Hughes 1998; Brewbaker 2016). Further germplasm collection, conservation, multiplication and evaluation of these taxa are required. In addition, recent advances in *Leucaena* taxonomy (Abair et al. 2019) and the use of molecular markers will enable the accurate description of germplasm currently held (often misidentified and/or duplicated) in international collections and facilitate a much-needed update of the World Leucaena Catalogue (Bray et al. 1997). The World Leucaena Catalogue could be promoted as a 'source of truth' for the identification of *Leucaena* spp. accessions exchanged for use in future breeding programs. Germplasm collections are expensive to maintain, as seed needs to be refreshed and multiplied. Seed of some species, e.g. *L. esculenta*, appears to have a shorter lifespan under long-term storage.

A number of important practicalities must be considered when formulating *Leucaena* spp. breeding programs, including: focussing on forage quality for multipurpose tree legumes to ensure the forage produced fattens animals; long-term field testing of interspecific hybrids or elite lesser-known species to ensure longevity under frequent cutting or heavy grazing; determining the promiscuity of new cultivars for *Rhizobium* spp. to facilitate effective nodulation and adequate rates of biological nitrogen fixation (Mullen et al. 1998); estimating the cost of producing propagules (seed vs. vegetative planting material) at a commercial scale suited for adoption in target farming systems; and understanding the environmental requirements and establishment practices (seed vs. vegetative planting material) required for rapid widespread adoption of new cultivars.

Finally, a key challenge to breeding *Leucaena* is the long time-frame (>10 years) and significant resources (financial and human) required to develop new cultivars. Collaboration between international breeding programs would make the most of these limited resources. Such collaboration may include: the exchange of successful breeding technologies/techniques and elite germplasm; and undertaking coordinated G × E trials of advanced breeding lines and emerging cultivars. The spirit of such collaboration has been epitomized by Professor James L. Brewbaker (University of Hawaii), who for over 50 years has generously shared his vast knowledge of *Leucaena* spp. collection, genetics and breeding plus elite germplasm with plant breeders around the world.

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(Note of the editors: All hyperlinks were verified 17 April 2019.)

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