



# Giant leucaena (*Leucaena leucocephala* subsp. *glabrata*): a versatile tree-legume for sustainable agroforestry

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**Abstract** *Leucaena leucocephala* (leucaena) is one of the 22 *Leucaena* species that originated in Central America. There are two major subspecies of leucaena, *L. leucocephala* subsp. *glabrata* (giant leucaena) and *L. leucocephala* subsp. *leucocephala* (common leucaena). Giant leucaena is a medium size fast-growing tree important for agroforestry while common leucaena is a small bushy shrub that is considered to be an invasive weed. Giant leucaena can be grown as a woody tree of up to ~ 20 m in height or maintained as a bushy fodder legume by repeated harvest of its foliage several times a year. Giant leucaena grown for fodder can produce forage dry mater yield of up to 34 Mg ha<sup>-1</sup> year<sup>-1</sup>. High forage yield together with high protein content makes leucaena an ideal fodder legume for the tropical and subtropical regions of the world. Although mimosine present in the leucaena foliage has toxicity, it should not be a big concern because ruminants can be successfully inoculated with the mimosine-metabolizing rumen bacterium

*Synergistis jonesii*. Alternatively, mimosine present in the leucaena foliage can be removed easily and inexpensively through simple processing. Giant leucaena cultivars are generally free from diseases and are highly tolerant to drought. Although infestation by psyllids may be a problem, a number of psyllid-resistant cultivars of giant leucaena have been developed through interspecies hybridization. The wood of giant leucaena can be used for timber, paper pulp, or biofuel production. Leucaena foliage and wood may serve as raw materials for development of new industry for production of phytochemicals such as mimosine, tannins and anthocyanins, wood products, and high-protein animal feed for farm animals in the future.

**Keywords** Giant leucaena · Fodder tree legume · Mimosine · Psyllid resistance · Drought tolerance · Agroforestry

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## Introduction

*Leucaena leucocephala* (leucaena) is a nitrogen-fixing tree-legume suitable for sustainable agroforestry systems. Leucaena grows successfully in a wide range of tropical and subtropical areas of the world where minimum daily temperatures are above 15 °C, including Central and South America, Africa, southern states

of USA, Australia, the Philippines, Thailand, Indonesia, South-East Asia, and the Pacific Islands. There are two major types of leucaena: giant leucaena that can grow as large trees with a height of up to 20 m and common leucaena that grows as a shrubby and invasive weed (Fig. 1). Interestingly, giant leucaena can also be grown and maintained as a shrubby and high-yielding nutritious fodder for farm animals. The aim of this review is to provide a comprehensive discussion on the genetics, characteristics, cultivation practices, utilities, improved varieties, and uses of leucaena.

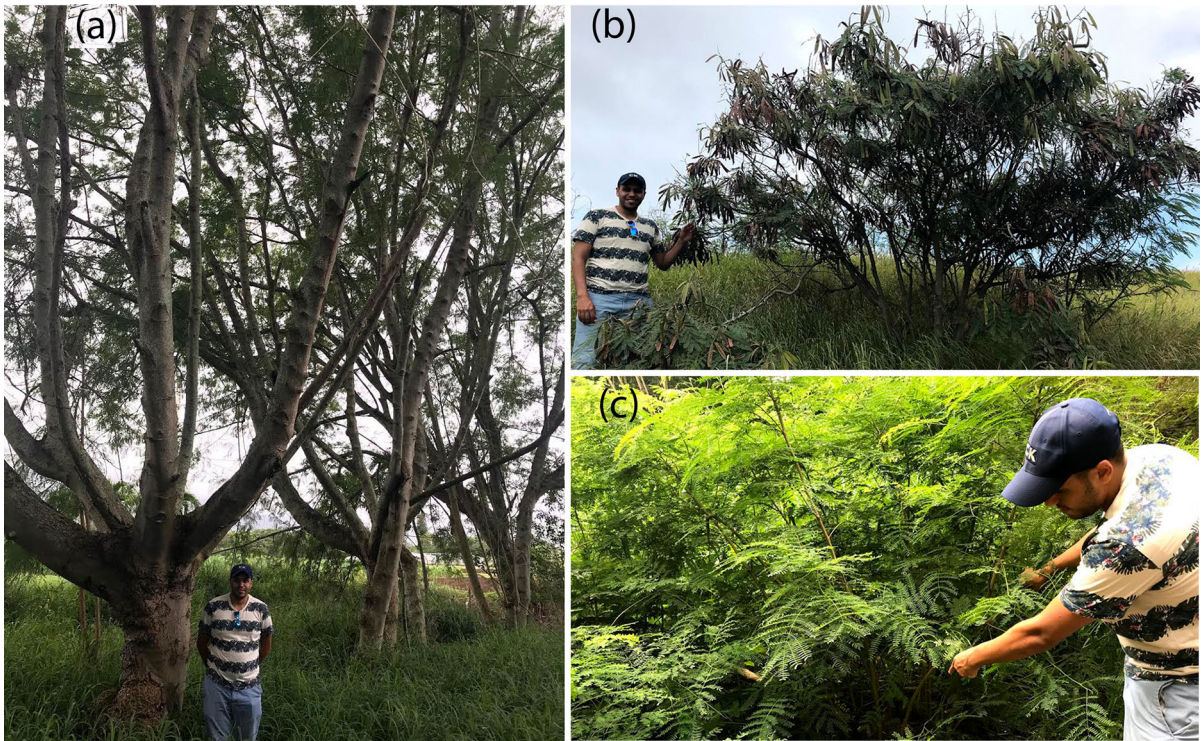
## Genetics

The genus *Leucaena* belongs to Mimoseae tribe, subfamily Mimosoideae in the Leguminosae family. There are twenty-two identified *Leucaena* species; most of them are diploid having 52 or 56 chromosomes ( $x = 26$  or  $x = 28$ ). The different *Leucaena* species and their characteristics are briefly described

in supplementary Table S1. There are also five tetraploid species ( $2n = 4x$ ): *L. leucocephala*, *L. diversifolia*, *L. pallida*, *L. confertiflora*, and *L. involucrata*. Among these, *L. leucocephala*, *L. pallida*, and *L. involucrata* are known to be allotetraploids, while *L. diversifolia* and *L. confertiflora* are considered to be autotetraploids. *L. leucocephala* is an allotetraploid, which evolved through natural hybridization between *L. pulverulenta* and *L. lanceolate* (Pan and Brewbaker 1988). The distribution of the *Leucaena* species is presented in supplementary Table S2.

## Giant leucaena versus common leucaena

*L. leucocephala* subsp. *glabrata*, also, known as giant leucaena, has glabrous leaflets (Hughes 1998a). In subsp. *glabrata*, some leaflets contain fine ciliate hairs along their margins towards the petiolule, and sparse hairs may be found on the rachis (SA Harris, personal communication). The natural populations of subspecies *glabrata* are widely distributed in Tehuantepec



**Fig. 1** Giant and common leucaena. **a** Giant leucaena trees at the Waimanalo Research Station, University of Hawaii; **b** common leucaena plants growing on a barren land in Hawaii

Kai, Honolulu showing its seediness characteristic; and **c** giant leucaena plants maintained as a bush shrub through repeated harvest of the foliage every few months

and northern Veracruz, Mexico (Zárate 1999). Subspecies *glabrata* includes two different types, Peru and Salvador, which originated in Peru and El Salvador regions of South and Central America, respectively. The trees of both Peru and Salvador types are tall and high yielding, but they differ in branching behavior and vigor. The Peru type branches low down on the trunk while the Salvador type branches sparingly at the base. Generally, the Salvador type is more vigorous and matures earlier than the Peru type. The Peru type cultivars are generally more suitable and productive as forage than the Salvador type (Zarate 1984). K8, K28, K29, K67, and K72 are examples of ‘Salvador type’ cultivars, while K5, Cunningham, and Peru are examples of Peru-type cultivars of giant leucaena. Because it is a multipurpose tree with various applications in industry, agriculture, and agroforestry, *L. leucocephala* subsp. *glabrata* is the most important and most studied among all *Leucaena* species. Because of its high productivity and worldwide success during the 1970s and early 1980s, giant leucaena was once called a ‘miracle tree’ (Shelton and Brewbaker 1994). It grows successfully in a wide range of tropical environments, and shows high tolerance to various environmental stresses including drought, infection by microbial pathogens, and insect pests. Although giant leucaena naturally grows as medium-sized tall trees, it can be also maintained as dwarf shrubs for fodder by repeated harvest of the foliage several times a year. The natural populations of subspecies *glabrata* are distributed in Mexico, Tehuantepec and northern Veracruz (Walton 2003).

*L. leucocephala* subsp. *leucocephala*, also known as common leucaena, in general, has smaller leaflets, leaves and pods than subsp. *glabrata*. Shoots, leaves and pods of common leucaena are sparsely pubescent with very fine soft hairs. Its major differentiating characteristics with giant leucaena are summarized in Table 1. Common leucaena has a much shorter vegetative growth stage in comparison to giant leucaena. Compared to the tall and big size of giant leucaena, common leucaena is a small bushy shrub that forms a lot of seeds, because of which it can spread easily and is considered invasive. It is an aggressive colonizer of ruderal sites, disturbed and degraded habitats, and occasionally agricultural lands. In Hawaii, it is classified amongst the 12 worst pests out of 86 serious alien invaders (Cronk and Fuller 1995). The name “koa haole” is generally used to

describe common leucaena, which originated in Southern Mexico or Guatemala (Wheeler and Brewbaker 1988). Morphological observations and limited isozyme studies in Hawaii did not reveal much variations among the populations of common leucaena suggesting that common leucaena is made up of a single genotype (Sun 1996; Brewbaker 2016). The subspecies *leucocephala* has the same distribution path as *glabrata*, which includes Mexico, Tehuantepec and northern Veracruz (Walton 2003).

### Leucaena germplasm and cultivars

Two major leucaena improvement programs based on systematic germplasm collection and evaluation started independently in two locations, one at the CSIRO Research Station, near Brisbane, Australia in late 1950s and the other at the Waimanalo Research Station, University of Hawaii in early 1960s (Brewbaker 2016). In 1962, Brewbaker and his colleagues collected 347 accessions of common leucaena from different parts of the world. They also made six expeditions in Latin America and collected ~ 500 accessions of giant leucaena. The leucaena germplasm collection by Brewbaker, known as ‘the Hawaii Collection’ contains a total of 1100 accessions including 967 from Central America. The leucaena germplasm collection in Australia, known as the ‘CSIRO Collection’ contained 815 accessions (Hughes et al. 1995). Hughes from Oxford Forestry Institute in UK made explorations for leucaena seed collection from Central America in mid 1980s. His collection, known as ‘the Oxford collection’, included seeds from a total of 1116 trees comprising 99 provenances that included all 22 species of *Leucaena* (Hughes et al. 1995).

Evaluation of the leucaena germplasm from Central America showed that *L. leucocephala* subsp. *glabrata* as the most significant leucaena for agriculture (Brewbaker 2016). Seventy-two accessions of giant leucaena were planted in a duplicate trial in Waimanalo, Hawaii and a number of outstanding giant leucaena lines, including K8, K28, K29, K67, K72, K584 and K636 were selected from these accessions. Some of the giant leucaena accessions in the Hawaii Collection grew to mature heights of about 45 feet in 4 years, and had high-quality wood and fodder (Brewbaker 2010). The cultivar “Hawaiian Giant

**Table 1** Differentiating characteristics between giant leucaena (*L. leucocephala* subsp. *glabrata*) and common leucaena (*L. leucocephala* subsp. *leucocephala*)

Characteristics	Giant leucaena	Common leucaena
General features	Medium size tree that can grow up to 20 m in height; can be maintained as a shrub by repeated pruning of its foliage 3–10 times a year	Bushy shrub, low growing, highly branched, 3–5 m in height
Seed production <sup>a</sup>	Produces relatively less pods and seeds	Produces a lot of pods and seeds
Young shoots <sup>a</sup>	Glabrous	Velutinous
Leaflets <sup>a</sup>	16–21 mm long	9–13 mm long
Capitula <sup>a</sup>	> 18 mm in diameter	12–17 mm in diameter
Young pods <sup>a</sup>	Glabrous	Sparsely pubescent

<sup>a</sup>Information obtained through personal communication from SA Harris, Oxford Forestry Institute

K8” was selected from the progenies of line K8 with emphasis on wood and forage yields (Brewbaker 2016). Leucaena cultivars K5 and K500, were introduced to Hawaii from Australia (Brewbaker 2016). K5 is a highly branching, Peru type cultivar of *L. leucocephala* subsp. *glabrata*, whereas K500 is a *L. leucocephala* subsp. *glabrata* Salvador type cultivar that originated from a cross made between the Salvador type and the more branched Peru type of *L. leucocephala* subsp. *glabrata* in Australia. Some of the promising cultivars of giant leucaena are listed in Table 2.

### Molecular biology studies in leucaena

Among the *Leucaena* species, the molecular biology of only *L. leucocephala* has been studied. Ishihara et al. (2016) analyzed transcriptomes of *L. leucocephala* subsp. *glabrata* cultivar K636 through Illumina-based sequencing and de novo assembly, which generated 62,299 and 61,591 unigenes from the root and shoot, respectively. Through a microarray analysis of more than 10,000 unigenes, they identified a number of genes that were highly expressed in the root compared to the shoot. A terpenoid biosynthesis gene, and nicotianamine synthase were two genes found to be upregulated more than 100-fold in the root, indicating that these genes may have important roles in the root. Similarly, through microarray analysis, Honda et al. (2018) identified 73 and 39 drought-responsive gene sequences in cultivar K636 that were upregulated in the root and shoot, respectively. They also validated the expression of some of the drought-

responsive genes by qRT-PCR analysis. Honda and Borthakur (2019) identified a number of genes that were highly expressed in the foliage of giant leucaena compared with the roots and postulated that these genes may contribute to the nutrient richness of leucaena foliage. Only a few leucaena genes have been cloned and characterized so far (Table 3). Kaomek et al. (2003) cloned cDNAs encoding two antifungal chitinases from *L. leucocephala* and expressed one of them in *E. coli*. The recombinant leucaena chitinase hydrolyzed colloidal chitin and inhibited growth of 13 of the 14 fungal strains tested. Shaik et al. (2013) cloned and characterized a leucaena gene encoding a glycosylhydrolase and analyzed its spatial and temporal expression by qRT-PCR in shoot and root tissues of young seedlings. Leucaena gene sequences for phenylpropanoid pathway enzymes leading to monolignol biosynthesis have been characterized to varying extents. The complete protein coding sequences have been identified for eight genes encoding important steps in monolignol biosynthesis (Khan et al. 2012). The individual downregulation of four of the monolignol biosynthesis genes (Cinnamate 4-Hydroxylase C4H), cinnamoyl CoA reductase, coniferaldehyde 5-hydroxylase, cinnamyl alcohol dehydrogenase (CAD) by antisense strategies resulted in reduced lignin content and stunted seedling growth (Khan et al. 2012). Reduced expression of one of the monolignol biosynthesis genes, 4-coumarate CoA ligase 1 (4CL), did not affect growth of leucaena seedlings although lignin content was reduced. Omer et al. (2013) cloned and characterized a leucaena cDNA for a R2R3-type MYB transcription factor gene, which is a regulator of the phenylpropanoid pathway and a general

**Table 2** Promising cultivars of giant leucaena

Variety <sup>a</sup>	Parent species	Characteristics	References
K5	<i>L. leucocephala</i> subsp <i>glabrata</i> cultivar of Peru type	Highly-branched; high biomass yields; high seedling vigor; susceptible to psyllids	Brewbaker (2016)
K8 or Hawaiian Giant	One of the <i>L. leucocephala</i> subsp. <i>glabrata</i> accessions collected from Zacatecas, Mexico	Most widely grown leucaena cultivar in the world. Vegetative vigor; aggressive arboreal growth, high leaf and wood yield. Grown in the Philippines for charcoal and fuel, and in Hawaii as a windbreak. When harvested for forage every 8–12 weeks it has produced much higher forage yields than other common cultivars; susceptible to psyllids	Brewbaker (1975)
K28	One of the <i>L. leucocephala</i> subsp. <i>glabrata</i> accessions collected from El-Salvador	Multipurpose cultivar; high foliage and wood yield; high seedling vigor; tolerant to acidic soils; widely distributed and considered superior in wood yields to K8. Reported to perform marginally better than K636 in acid soils	Brewbaker and Hylin (1965)
K29	One of the <i>L. leucocephala</i> subsp. <i>glabrata</i> Salvador type accessions collected from Honduras	Multipurpose cultivar; high foliage and wood yield; high seedling vigor; low seediness but full male fertility; difficult for seed multiplication	Brewbaker and Hylin (1965)
K67	One of the <i>L. leucocephala</i> subsp. <i>glabrata</i> Salvador type accessions collected from El-Salvador	High foliage and wood yield; high seed production; high seedling vigor; similar to K8 in foliage yield	Brewbaker et al. (1972)
K132	One of the <i>L. leucocephala</i> subsp. <i>glabrata</i> Peru type accessions collected from Zacatepec, Morelos, Mexico	Lower in branching; large pods favored as food source; high foliage and wood yield	Brewbaker (2016)
K500 or Cunninghamham	Selected in Australia from the progeny of a cross between Salvador and Peru types of <i>L. leucocephala</i> subsp. <i>glabrata</i>	High foliage and wood yield; cold tolerant; psyllid susceptible	Rengsirikul et al. (2011)
K584	One of the <i>L. leucocephala</i> subsp. <i>glabrata</i> accessions collected from Veracruz, Mexico	Combined stature of both Salvador and Peru type; has a form similar to K636 but has more branching like the Peru type; highly resistant to psyllids	Brewbaker (2016)
K636 or Tarramba	One of the <i>L. leucocephala</i> subsp. <i>glabrata</i> accessions collected from Coahuila, Mexico	High forage yield; high seedling vigor; cold tolerant; low branching; moderate psyllid resistance; less seedy, difficult for seed multiplication; low tannin content	Brewbaker (1987)
K748	Interspecies hybrid variety <i>L. pallida</i> × <i>L. leucocephala</i>	High forage and wood yields; highly resistant to psyllids; high seedling vigor; high seed production	Austin et al. (1997)
K1000	Interspecies hybrid variety between <i>L. esculenta</i> × <i>L. leucocephala</i> subsp. <i>glabrata</i>	High seedling vigor; sterile; cold tolerant; highly resistant to psyllids	Hughes (1998b)
KU19	F3 line selected from the F2 hybrid of <i>L. leucocephala</i>	High foliage and wood yields	Rengsirikul et al. (2011)
KU66	F3 line selected from the F2 hybrid of <i>L. leucocephala</i>	High foliage and wood yields	Rengsirikul et al. (2011)
KX2	Interspecies hybrid variety between <i>L. leucocephala</i> and <i>L. pallida</i>	Highest biomass yield High seedling vigor; highly resistant to psyllids; low seed production; self-incompatibility; high digestible; low tannin content	Mullen et al. (2003), Jones and Palmer (2002)

**Table 2** continued

Variety <sup>a</sup>	Parent species	Characteristics	References
KX3	Interspecies hybrid variety between <i>L. diversifolia</i> × <i>L. leucocephala</i>	High forage yields; high seedling vigor; highly resistant to psyllids; cold and frost tolerant; self-fertile	Mullen and Gutteridge (2002)
KX4	Triploid hybrid between <i>L. esculenta</i> and <i>L. leucocephala</i> subsp. <i>glabrata</i>	High foliage and wood yields, fast growing; seedless, lack pods; good wood quality; highly resistant to psyllids; highly tolerant to drought	Brewbaker (2013)
Lanang or Male Leucaena	Spontaneous hybrid between <i>L. leucocephala</i> and <i>L. pulverulenta</i> , selected in Indonesia	Fast growing; variable sterile; high nutritive value; low mimosine content; high seedling vigor; high wood yields; psyllid susceptible	Hughes (1998b)
Peru	Peru type variant of <i>L. leucocephala</i> subsp. <i>glabrata</i>	High foliage and wood yields production	Rengsirikul et al. (2011)
Redlands	Developed in Australia from the progeny of a cross between <i>L. leucocephala</i> and <i>L. pallida</i>	Highest biomass yields, highly resistant to psyllids; high tannin content; medium dry matter digestibility	Lambrides (2017)
Rendang	Developed in Malaysia from a cross between <i>L. leucocephala</i> subsp. <i>glabrata</i> × <i>L. diversifolia</i>	Few seeds; highly resistant to psyllids; good dry matter digestibility; moderately cool tolerant	Zarin et al. (2016)
Wondergraze	A selection from the progeny of a cross between <i>L. leucocephala</i> subsp. <i>glabrata</i> variety K636 with K584	High seedling vigor; shorter stature, basal branching, and more bushy like the Peru type; similar to K636 for psyllid and cold tolerance; high forage yield; good forage quality and palatable	Brewbaker (2016)

<sup>a</sup>Cultivars with the prefix ‘K’, ‘KX’, and ‘KU’ were developed in Hawaii

repressor of lignin biosynthesis. Overexpression of the leucaena MYB using a strong constitutive promoter, CaMV35S, in transgenic tobacco resulted in significant downregulation of early phenylpropanoid pathway genes phenylalanine ammonia lyase, C4H, 4CL, and CAD. Downregulation of these lignin precursor genes may help to reduce the lignin content of leucaena.

Leucaena genes related to mimosine synthesis, degradation, and transport are of particular interest because of the toxic effects of mimosine and its degradation products 3,4-dihydroxypyridine (3,4-DHP) or its isomer 3-hydroxy-4-pyridone (3H4P). Transgenic leucaena expressing *Rhizobium* sp. strain TAL1145 gene *pydA* exhibited up to a 22.5% reduction in mimosine content (Jube and Borthakur 2010). Negi et al. (2014) cloned the cDNA for mimosinase from giant leucaena K636 and expressed it in *E. coli*. The purified recombinant mimosinase degraded mimosine into 3H4P, pyruvate and ammonia. The mimosine-degrading enzyme activity of mimosinase

is very similar to that of rhizomimosinase (Negi et al. 2013).

Genes related to environmental stress response (Negi et al. 2011) require further investigation as leucaena is an extremely resilient to most abiotic stresses. Out of 15 hypothetical proteins identified as a response to prolonged drought, the complete coding sequence is known for only metallothionein. Further identification and characterization of stress-related genes in leucaena may prove valuable in increasing stress tolerance of other crops.

### Total biomass and forage yields of giant leucaena

The biomass and forage yields of leucaena can vary considerably depending on climatic conditions, cultural practices, season, location, and occurrence of psyllids. The forage yield of giant leucaena is 2.5 times higher than that of common leucaena (Brewbaker 1975). Guevara et al. (1978) showed that total dry matter and forage dry matter yields of giant leucaena

**Table 3** *L. leucocephala* genes that have been cloned and characterized

Gene	Accession no.	Description	References
Phenylalanine ammonia lyase (PAL)	JN540043.1	A partial cDNA (1.1 kb) of an expected ~ 2 kb coding sequence was sequenced	Khan et al. (2012)
Cinnamate 4-Hydroxylase (C4H)	JN874563.1 HQ191221.2 HQ191222.2	Three highly similar alleles of LICH41 gene were isolated and transcription levels measured by qPCR in various tissue types of different ages. Antisense-LICH41 expression resulted in stunted growth	Kumar et al. (2013)
4-coumarate CoA Ligase 1 (4Cl)	FJ205490.1	Transgenic leucaena containing antisense-4Cl construct showed 2–7% reduction in lignin content but no detectable change in morphology	Gupta (2008)
Caffeoyl-CoA-O-methyltransferase (CCoAOMT)	DQ431233.1 DQ431234.1	Isolation and cloning of two leucaena CCoAOMT isoforms described. Three-dimensional models were proposed based on either isoform to predict interaction with substrate	Pagadala et al. (2009)
Cinnamoyl CoA reductase (CCR)	EU195224.2 DQ986907.3	Spatial expression of LI-CCR analyzed by qRT-PCR and ELISA with respect to lignification over time	Srivastava et al. (2011)
Coniferaldehyde 5-hydroxylase (Cald5H)	EU041752.1	Transgenic leucaena and tobacco were made using sense and antisense strategies respectively. Transgenic leucaena expressing antisense-Cald5H construct did not show morphological changes	Yadav (2009)
Cinnamyl alcohol dehydrogenase (CAD)	EU870436.1	Cloned, expressed in <i>E. coli</i> , and purified the recombinant leucaena CAD for kinetic studies	Pandey et al. (2011)
Caffeic acid O-methyltransferase (COMT)	EF611249.1	Cloned, expressed in <i>E. coli</i> , and purified the recombinant leucaena LIOMT in <i>E. coli</i> . The purified protein used for enzyme kinetics and activity studies	Dwivedi et al. (2014)
Peroxidase (POX)	EU649680.1	Leucaena POX was purified in native form from stem tissue, characterized and assayed	Pandey and Dwivedi (2011)
Cellulose synthase	FJ871987.2 GQ267555.2	Tissue specific differential expression of two isoforms (LI-7CesA and LI-8CesA) were studied in root, stem, and leaves by qRT-PCR	Vishwakarma et al. (2012)
MYB transcription factor gene	GU901208.1	Isolated and characterized a R2R3-type MYB transcription factor gene, which is a regulator of the phenylpropanoid pathway and a general repressor of lignin biosynthesis	Omer et al. (2013)
β-carbonic anhydrase	KC924756.1 KC924757.1	Chloroplastic (cacp) and cytoplasmic (cacyt) isoforms of leucaena β-carbonic anhydrase were isolated, structurally analyzed in silico, and transcription levels were compared under various abiotic conditions in different tissues	Pal and Borthakur (2014)
Metallothioneine	KC355441.1	One of the 15 hypothetical proteins identified by interspecies suppression subtractive hybridization (iSSH); it was upregulated 48-fold under drought conditions	Negi et al. (2011)
Mimosinase	AB298597.1	Isolated, cloned, expressed in <i>E. coli</i> and purified the recombinant mimosine-degrading enzyme from leucaena. Conducted biochemical characterization of the enzyme and degradation products of mimosine	Negi et al. (2014)
Cy-O-acetylserine thiol lyase	KF754356.1	Isolated, cloned, expressed in <i>E. coli</i> and purified the recombinant leucaena cy-OAS-TL. The recombinant enzyme catalyzed synthesis of cysteine but not of mimosine	Yafuso et al. (2014)
Chitinase	AF513017.2	Isolated and cloned cDNAs for two leucaena chitinases. One of the chitinases was expressed in <i>E. coli</i> and the purified protein was shown to have chitinase activities	Kaomek et al. (2003)
Glycosylhydrolase I	EU328158.1	Cloned and characterized the recombinant enzyme by glycone specificity and kinetic properties. Spatial and temporal expression analysis by qRT-PCR was performed on shoot and root tissues of young seedlings	Shaik et al. (2013)

depend on a number of factors including growing season, cultivar, spacing, cutting height, and cutting intervals. Based on their experimental results, they recommended a cutting height of 25–35 cm above ground and cutting interval of 3 months for obtaining optimum forage yield. The forage dry matter yield of giant leucaena cultivar Peru in one set of experiments conducted in Mexico was  $6.9 \text{ Mg ha}^{-1} \text{ year}^{-1}$  (Casanova-Lugo et al. 2014), which was much lower than the average forage dry matter yield of  $26.6 \text{ Mg ha}^{-1} \text{ year}^{-1}$  from three Salvador type of giant leucaena cultivars (K8, K28 and K67) grown in Hawaii (Brewbaker et al. 1972). Austin et al. (1995) reported a total dry mater biomass yield and a forage dry mater yield of up to 63.7 and  $34 \text{ Mg ha}^{-1} \text{ year}^{-1}$ , respectively, for giant leucaena grown in Hawaii. Mullen and Gutteridge (2002) observed that the total dry mater biomass yield of the interspecies leucaena hybrids KX2 and KX3 could be as high as  $84 \text{ Mg ha}^{-1} \text{ year}^{-1}$ . They suggested that the high yields of KX2 and KX3 could be the result of heterosis and high psyllid resistance of the hybrids.

### Nutritional properties of leucaena

Leucaena is considered an important fodder legume due to its palatability and high protein content in the foliage. Because of its high nutritional value, it is often referred to as the ‘alfalfa of the tropics’. Young shoots have up to 31% protein on a dry weight basis, which decreases to 14% after 10 weeks (Tangendjaja et al. 1986). Garcia et al. (1996) reviewed 65 publications between 1946 and 1992 for nutritive value and forage productivity of leucaena and found that the medial concentration of crude fiber and crude protein was 19.2% and 29.2%, respectively. Soedarjo and Borthakur (1996b) found that young leucaena leaves of common leucaena contained only  $\sim 18\%$  protein. They suggested that protein concentrations might have been overestimated in some of the earlier reports, because mimosine, a non-protein amino acid, present in the samples interacts with the reagents for protein estimation, giving an overestimate of the protein content. They also described a more accurate method of determining soluble protein content in leucaena tissues containing mimosine. In spite of having high protein contents and high palatability, leucaena foliage has two negative attributes: (1) it has high

amounts of mimosine, which is toxic to animals, and (2) it has high amounts of condensed tannin, which has been identified as a major factor limiting the nutritive value of leucaena foliage (Wheeler et al. 1995; Garcia et al. 1996; Osborne and McNeill 2001; Chanchay and Poosaran 2009). The mimosine contents of different parts of the shoot vary from 1 to 12%; the growing tips contain the highest amounts while the old stems contain the lowest amounts (Jones 1979). Young leaves contain  $\sim 4.5\%$  mimosine on a dry weight basis, which decreased to  $\sim 2\%$  in 10-week-old leaves (Tangendjaja et al. 1986). Chanchay and Poosaran (2009) also found 4.4% mimosine in the leaves of leucaena. Soedarjo and Borthakur (1996a) determined that young leaves and pods of leucaena contained as high as 6–10% mimosine on a dry weight basis. Condensed tannins are polyphenolic compounds that bind with soluble proteins and make them insoluble and indigestible. Leucaena leaves contain 1–5% total tannin, comprising both hydrolysable and condensed tannins (A. Bageel and D. Borthakur, unpublished results).

### Functions of mimosine in leucaena

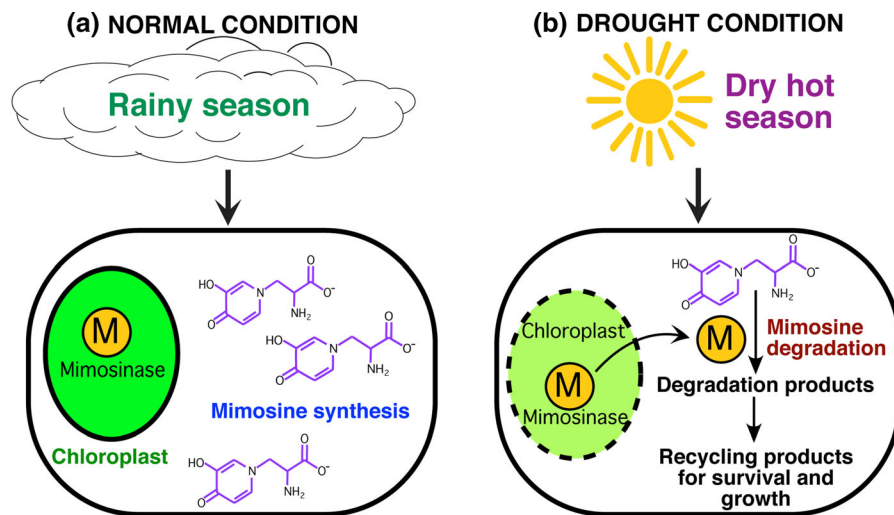
The toxic non-protein amino acid mimosine is present in all leucaena species and is generally considered as a chemical defense mechanism against various biotic stresses. Mimosine, its degradation product 3H4P, and substituted derivative ‘mimosinol’ have been studied for their nematocidal, insecticidal, herbicidal, and antimicrobial properties (Anitha et al. 2005; Xuan et al. 2006, 2013; Tawata et al. 2008; Nguyen et al. 2015; Xuan et al. 2016). Mimosine was also found to inhibit germination of rice and albizziine seeds (Prasad and Subhashini 1994; Williams and Hoagland 2007). Leucaena extracts, which contain a high amount of mimosine have been shown to have anthelmintic and acaricidal properties (Kabore et al. 2012; Ademola and Idowu 2013; Auamcharoen and Chandrapatya 2015). Soedarjo et al. (1994) showed that inhibitory effects of mimosine on bacterial growth are bacteriostatic and not bacteriocidal. Mimosine is known to chelate multivalent metal ions such as  $\text{Fe}^{3+}$ ,  $\text{Zn}^{2+}$ ,  $\text{Cu}^{2+}$ ,  $\text{Ni}^{2+}$ ,  $\text{Co}^{2+}$  and  $\text{Mn}^{2+}$  that serve as cofactors for many enzymes. By chelating these ions, mimosine inactivates these enzymes and thereby inhibits bacterial growth. Mimosine also binds to



pyridoxal 5'-phosphate (PLP), and thereby inhibits all PLP-requiring enzymes such as decarboxylases, amino acid transferases, lyases, tryptophan synthase, cysteine synthase etc. in microorganisms, and thus prevents their growth. As previously mentioned, the mimosine content of leucaena foliage can be as high as 10%. Negi et al. (2014) estimated that if the total carbon and nitrogen used for production of mimosine were diverted for growth, the leucaena tree would have grown at least 21% larger. They also proposed that mimosine may provide a mechanism of drought resistance in leucaena. According to this idea, during favorable weather conditions, when water and nutrients are available, leucaena synthesizes mimosine and accumulates in different parts of the plant, including the foliage. Under drought conditions, mimosine is degraded by the enzyme mimosinase present in chloroplasts. They further suggested that during drought conditions, some chloroplasts membrane may be broken down, and mimosinase from the chloroplast stroma come in contact with mimosine in the cytoplasm (Fig. 2). Recent experimental results showed that mimosine concentration in leucaena foliage was increased when plants were grown with added nitrogen but reduced under prolonged drought treatment (Honda and Borthakur, unpublished results).

## Tolerance to drought stress

Leucaena can grow successfully in soils with low nutrient and moisture availability. It can survive drought conditions for several months during a prolonged dry season and recover quickly with availability of water (Shelton and Brewbaker 1994). Attributes of root competitiveness, such as taproot length, lateral root length density, mycorrhizal colonization, nodulation and nitrogen fixation, disease resistance, and flexibility in response to water and nutrient availability in the soil, are some of the important determinants of leucaena's success as a stress-tolerant tree legume in tropical and subtropical environments. Yige et al. (2012) showed that leucaena seedlings had the ability to maintain high levels of leaf water content (LWC), which did not decrease significantly until 9 days of drought. Ezenwa and Atta-Krah (1992) noted that leucaena seedlings grown in soils allocated more nutrient resources for growth of the taproot than on lateral roots until about 12 weeks. Leucaena is a deep-rooted species, which can extend its roots up to 5 m to exploit underground water (Brewbaker et al. 1972). This may be one of the reasons why leucaena is naturally resistant to drought. In dry areas, leucaena remains unaffected by drought as long as its deep roots can reach groundwater.



**Fig. 2** Mimosine may be recycled as a source of nutrients during drought. **a** During rainy season, when the environmental conditions for growth are favorable, leucaena leaves produce a lot of mimosine, which is stored in the cell cytoplasm. A mimosine-degrading enzyme, mimosinase, is located in the chloroplast and thus mimosine and mimosinase are separated by

chloroplast membranes. **b** However, under drought conditions some of these membranes may break, resulting in the release of mimosinase from the chloroplast to the cytoplasm, where mimosine is degraded by mimosinase. The degradation products of mimosine are recycled for survival and growth by the leucaena plant during drought (Negi et al. 2014)

*Leucaena* also shows avoidance responses toward drought condition through leaflet folding during dry spells to prevent water loss and by shedding some leaves under severe drought conditions (Brewbaker 1987). Rao et al. (2008) reported that the net photosynthetic rate and transpiration rate decreased and stomatal resistance increased in *leucaena* in response to high water stress. They also observed that under high water stress, *leucaena* maintained higher water potential and proline content, indicating drought resistance. *Leucaena* pastures also have been shown to have high water use efficiency compared with other pasture types (Dalzell et al. 2007). Once established, *leucaena* shows excellent erosion control characteristics. In many *leucaena* pastures, little runoff is observed even after high intensity rainfall (Shelton and Dalzell 2007).

### Infestation by insects

The psyllid pest *Heteropsylla cubana* is known to cause damage to *leucaena* plants by feeding on juvenile leaflets and causing defoliation (Funasaki et al. 1989). With a short life cycle of about 2 weeks and the ability to lay up to 400 eggs in their lifetime, this pest grows exponentially and quickly infests plants, especially in warm, moist conditions. Psyllid infestation on common *leucaena* was reported to be a serious problem in the Caribbean, Hawaii, Mexico, Philippines and Thailand (Othman and Prine 1984; Sorensson and Brewbaker 1984; Ahmed et al. 2014; Brewbaker 2016). Trials to test for psyllid tolerance in various *Leucaena* species were performed in Thailand, Mexico, Philippines, and USA (Brewbaker 2016). Also, efforts have been made to develop psyllid-resistant cultivars of giant *leucaena* by crossing them with *Leucaena* species that have higher resistance against the psyllid, such as *L. esculenta* and *L. pallida* (Brewbaker 2008). Interspecies hybrids KX2, KX3 and KX4 have been found to be resistant to psyllids. Currently, these psyllid-resistant hybrids are under agronomic trials in Hawaii and Australia. Other *leucaena* varieties that are selected for psyllid tolerance and extensively grown in Australia and Hawaii are Tarramba and Wondergraze (Brewbaker 2016).

Bruchid beetle (*Acanthoscelides macrophthalmus*) are host-specific seed destroying insects that can cause considerable damage to *leucaena*; it damaged up to

44% of *leucaena* seeds in Ethiopia (Yirgu et al. 2015). Interestingly, the bruchid beetle have also been used to restrict the invasiveness of legume trees including common *leucaena* in South Africa and Australia (Neser and Kluge 1986; Jones and Jones 1996). In Mexico, *leucaena* is naturally attacked by two genera of seed beetle, *Acanthoscelides* and *Sator*. There are five species of *Acanthoscelides* that feed on *leucaena* but do not attack any other plant species. *A. macrophthalmus* is known to attack 18 different species of *Leucaena*. With regard to genus *Sator*, it has two species, which attack a broad range of Mimosoid legume genera including *Leucaena* species (Hughes and Johnson 1996).

### Symbiotic nitrogen fixation

*Leucaena* forms nitrogen-fixing nodules in symbiosis with specific *Rhizobium* species such as *Rhizobium* sp. strain TAL1145 and *Rhizobium tropici* strain CIAT899 (Martínez-Romero et al. 1991; George et al. 1994). *Leucaena-Rhizobium* symbiosis is very specific. *Rhizobium* strains isolated from nitrogen-fixing root nodules of *leucaena* generally cannot form effective nodules on other legumes such as cowpeas, beans, peas, etc. (Trinick 1968). Under laboratory condition, strain TAL1145 can form only ineffective nodules on common bean (Borthakur and Gao 1996). In greenhouse experiments using the  $^{15}\text{N}$ -labelling method, *leucaena* was observed to have a consistently increasing pattern of nodulation, dry biomass accumulation, and nitrogen yield over a period of 16 months after planting (Kadiata et al. 1995). In field experiments, using the  $^{15}\text{N}$  isotope dilution and the total N difference methods, *leucaena* K636 was found to fix consistently high levels of atmospheric  $\text{N}_2$  even after third cuttings following 36 months of planting (Sanginga et al. 1989). Most of the *Rhizobium* strains that nodulate *leucaena* in Hawaii can degrade mimosine completely and use it as a source of carbon and nitrogen (Soedarjo et al. 1994; Soedarjo and Borthakur 1996a). TAL1145 was listed as a competitive strain for nodulation of *leucaena* in several reports (Moawad and Bohlool 1984; Somasegaran and Martin 1986; George et al. 1994). In competition experiments under field conditions using six indigenous *Rhizobium* strains on *leucaena* grown in oxisol and mollisol soils in Hawaii, strain TAL1145 was

found to be most competitive (Moawad and Bohlool 1984). Soedarjo and Borthakur (1998) constructed several mimosine-non-degrading ( $\text{Mid}^-$ ) mutants of TAL1145 and used them in competition experiments with TAL1145 on leucaena. The results of their experiments showed that the mimosine-degrading ability of strain TAL1145 provides a competitive advantage for nodulation of leucaena. By growing leucaena under hydroponic conditions, Soedarjo and Borthakur (1998) showed that some amount of mimosine is secreted in the leucaena root exudates. They proposed that mimosine in the rhizosphere binds with  $\text{Fe}^{3+}$  to produce mimosine- $\text{Fe}^{3+}$  complex, which is then taken up by *Rhizobium* and used as a source of nutrients. *Rhizobium* degrades mimosine into two molecules each of pyruvate, formate and ammonia (Borthakur et al. 2003, Awaya et al. 2005) (Fig. 3). Soedarjo and Borthakur (1998) also showed that mimosine is present in the leucaena root nodule, where it is used as a source of carbon and nitrogen by resident nodule rhizobia that have not differentiated into the nitrogen-fixing bacteroid form. The genes for mimosine degradation from TAL1145 have been isolated and characterized (Fox and Borthakur 2001; Borthakur et al. 2003; Awaya et al. 2005, 2007). Negi et al. (2013) characterized the protein encoded by the *midD* gene of TAL1145 and showed that it had enzymatic properties similar to mimosinase of leucaena. They named this *Rhizobium* enzyme as rhizomimosinase, which converted mimosine into 3H4P, pyruvate, and ammonia. Rhizomimosinase and mimosinase do not show much homology but both enzymes have similar mimosine-binding and PLP-binding domains (Negi et al. 2014).

### Agricultural and ecological benefits of giant leucaena

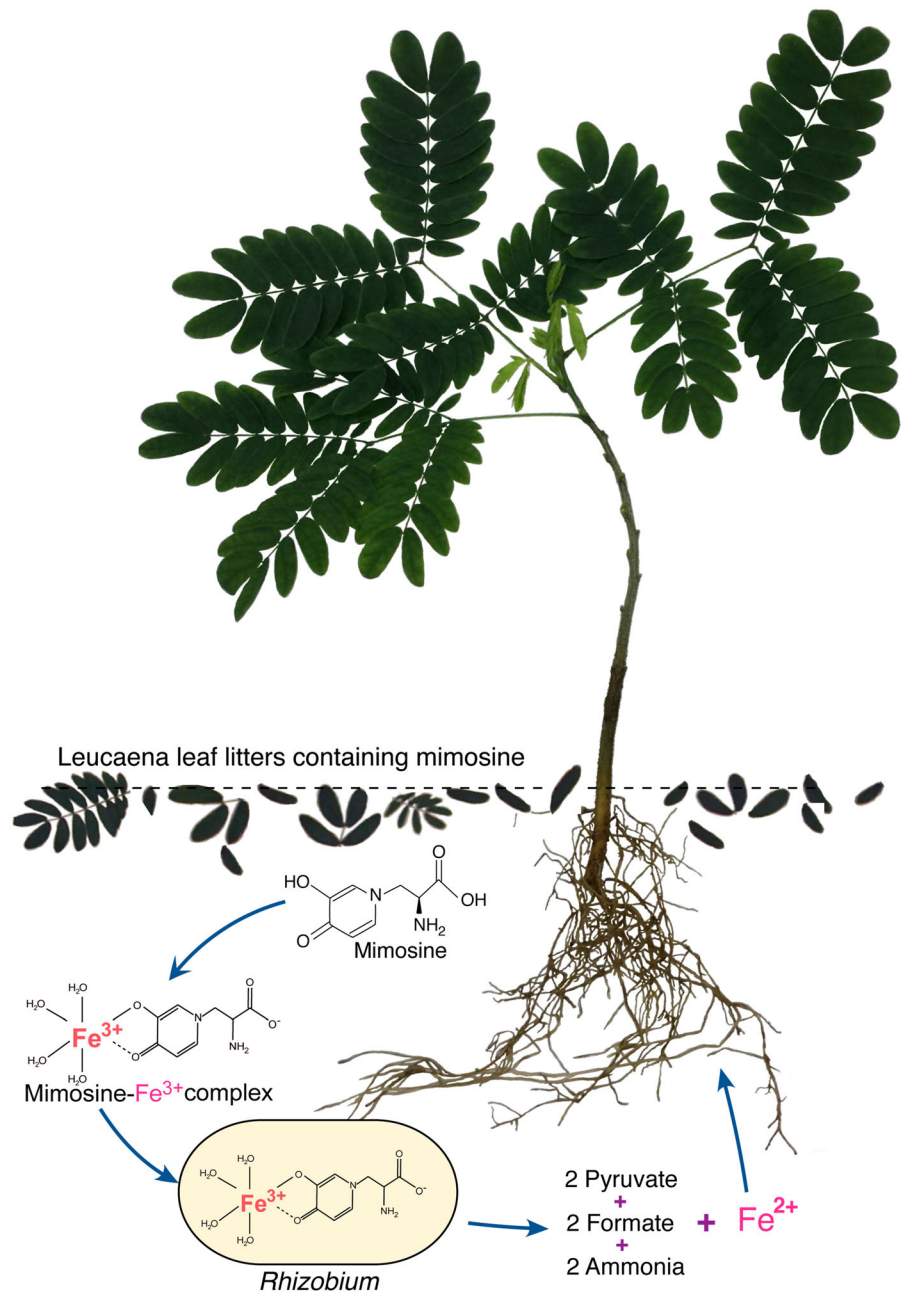
As previously mentioned, giant leucaena possesses a number of traits that are beneficial in various agroforestry systems. These traits include (1) high adaptability to a wide range of environmental conditions, including drought and alkaline soils, (2) tolerance to many biotic stresses, (3) accelerated growth, (4) high biomass yields, and (5) symbiotic relationship with nitrogen-fixing bacteria. The hardiness and rapid growth of giant leucaena make it a suitable hedgerow legume for alley cropping systems (Rosecrance et al.

1992). The height and diameter of teak tree (*Tectona grandis*) were increased when it was intercropped with leucaena (Kumar et al. 1998). Similarly, a number of studies utilizing leucaena in alley cropping systems with maize showed higher maize yields as well as other beneficial effects such as improved soil nutrient chemistry profile and even suppression of weed growth (Jama et al. 1991; Dalland et al. 1993; Xu et al. 1993a, b; Mureithi et al. 1994; Mugendi et al. 1999). Leucaena may also be used as a windbreak, live fence, live scaffold for growing vines like yam, or shade tree for production of coffee and cocoa (Hughes 2006; Youkhana and Idol 2011; Brewbaker 2013). When leucaena was planted as a windbreak, it was found to increase soil moisture availability as well as the grain yield of agricultural crops (Swaminathan 1987). When used in crop rotation, as an alley crop, cover crop, green manure, green mulch, or in cut-and-burn cultivation, leucaena can help to manage N cycling, increase organic carbon, and restore important nutrients like N, P, and K in the soil (Atta-Krah 1990; Xu et al. 1993a, b; Grewal et al. 1994; Heinemana et al. 1997; Kumar et al. 1998; Isaac et al. 2003). As a fast-growing nitrogen-fixing legume, leucaena is an ideal tree for reforestation of marginal lands and watersheds; and because it thrives in steep slopes, it can help to control soil erosion. Leucaena grows well in steep slopes where it effectively controls erosion by reducing surface run-off and soil loss (Dijkman 1950; Parera 1982; Celestino 1985; Grewal et al. 1994; Savale et al. 2007).

### Leucaena in phytoremediation

Leucaena has been researched as a possible tool in biological remediation of coal and metal mine tailings, tannery and dye pollutants, waste oil pollutants, lagoon ash, fly ash, textile waste, and heavy metal contaminated soils (Cheung et al. 2000; Gupta et al. 2000; Song et al. 2005; Bisht et al. 2011; Jayanthi et al. 2014; Edwin-Wosu and Nkang 2016; Ssenku et al. 2017). Leucaena has been shown to uptake, store, and to some degree, tolerate heavy metals such as arsenic, lead, chromium, cadmium, and nickel (Rout et al. 1999; Iqbal and Shazia 2004; Song et al. 2005; Shafiq et al. 2008; Sakthivel and Vivekanandan 2009; Dias et al. 2010; Ho et al. 2013; Adanikin and Kayode 2019). It was also found that leucaena biomass is a

**Fig. 3** A possible role of mimosine in the leucaena rhizosphere. Mimosine present in the leucaena leaf litters is released to the soil, where it binds with  $\text{Fe}^{3+}$  to form a mimosine- $\text{Fe}^{3+}$  complex, which is taken up by free-living rhizobia or other bacteria in the leucaena rhizosphere; rhizobia utilize mimosine by degrading it into two molecules each of pyruvate, formate, and ammonia. Rhizobia also converts  $\text{Fe}^{3+}$  to  $\text{Fe}^{2+}$  and release excess  $\text{Fe}^{2+}$  in the rhizosphere, where it is taken up by the leucaena roots



cheap and effective phytoadsorbent of various dyes present in contaminated waters (Karthikeyan and Rajendran 2010; Rajendran et al. 2015; Gayathri and Jayanthi 2016). Radrizzani et al. (2011) found that established leucaena-grass pastures accumulated enough organic carbon to offset the carbon dioxide produced from cattle, grazing on these same pastures.

## Conclusions

Giant leucaena has a combination of key attributes such as nitrogen-fixing ability, drought tolerance, easy cultivation, and high protein content of foliage because of which it is important for agroforestry. The future of giant leucaena as an agroforestry species depends largely on public understanding of the

difference between giant and common leucaena. Unfortunately, most people know leucaena as an invasive weed. They may not know that giant leucaena is not invasive as common leucaena and it is a valuable tree legume for high biomass productivity. The biomass produced by giant leucaena can be harnessed either as a nutritious fodder or as wood depending on the method of growing and harvesting. It can be grown either as a shrub by repeated harvest of the foliage several times a year or as a woody tree by allowing it to grow as a fast-growing medium-size tree. Giant leucaena produces much more vegetative growth and relatively few seeds while common leucaena produces a lot of seeds relative to its vegetative growth. Efforts must be made to bring farmers to experimental research stations or demonstration plots where giant leucaena is grown as a forage legume and also as a woody tree. By seeing the benefits of giant leucaena and its difference from common leucaena, farmers will understand why giant leucaena was once called a ‘miracle tree’.

Leucaena produces mimosine, which has some adverse effects on fodder quality. However, the presence of mimosine in the leucaena foliage may not be a big concern, because ruminants grazing on leucaena can be inoculated with the rumen bacterium *Synergistes jonesii*, which can detoxify mimosine (Jones and Megarrity 1986; Allison et al. 1992). Alternatively, mimosine present in the leucaena foliage can be removed, easily and inexpensively through simple processing and without significantly reducing the soluble protein content of the foliage. Soedarjo and Borthakur (1996b) observed that up to 97% mimosine in leucaena young leaves, pods, and seeds can be removed by soaking it in water for 24 h. The mimosine-free foliage can be then dried and fed to animals immediately, or converted into silage for future use. Additionally, the mimosine-free foliage can be processed, mixed with grasses and additional supplements, and developed into nutritious and palatable feed for all animals, including poultry, cows, sheep, goats, pigs, and fishes (Varvikko et al. 1992; Kaitho et al. 1996; Zakayo et al. 2000; Khan et al. 2009; Amisah et al. 2009).

There are variations among leucaena varieties for resistance to psyllids, which can cause heavy infestation in susceptible varieties. A number of *Leucaena* species such as *L. collinsii*, *L. confertiflora*, *L. esculenta*, *L. greggii*, *L. lempirana*, *L. matudae*, and

*L. pallida* are highly resistant to psyllids. Therefore, efforts have been made to develop psyllid resistant varieties through interspecies crosses of *L. leucocephala* subsp. *glabrata* cultivars with these species.

The wood of giant leucaena has been used for timber and high quality paper production in India (Prasad et al. 2011; Pandey and Kumar 2013). Giant leucaena may provide opportunities for new industries in the future. After extraction of mimosine from the leaves, the mimosine-free young leaves can be dried to produce herbal tea (Tawata et al. 2008). Mimosine extracted from leucaena and its degradation product 3H4P are used in biomedical research. 3H4P can be manufactured from mimosine, using a recombinant enzyme mimosinase or rhizomimosinase (Negi et al. 2013, 2014; Negi and Borthakur 2016). Considering its potential for use in industry, its use as a nutritious fodder, and its growing acceptance among farmers, giant leucaena may slowly replace common leucaena in many parts of the world.

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