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Article

TAXONOMIC APPRAISAL OF NODULATION IN THE LEGUMINOSAE OF PAKISTAN

Avaliação Taxonômica da Nodulação em Leguminosas do Paquistão

MAHMOOD, A.[1]
ATHAR, M.[1,2]*

ABSTRACT - Rhizobia are gram negative bacteria that infect roots of leguminous plants and form root nodules. Legume-rhizobia symbioses are of practical importance in providing sustainable food supply and increased agricultural productivity. Existing lists published on the nodulating ability of Pakistani legumes were merged to compile a comprehensive list. The list contained 225 species distributed in 75 genera that were native to Pakistan. Legumes were arranged according to the recommendations of International Legume Database and Information Center (ILDIS) for legumes of south Asia. Out of 225 species examined, 28 belonged to Caesalpinioideae, 29 belonged to Mimosoideae and 168 belonged to Papilionoideae. The percentage of nodulation in Caesalpinioideae, Mimosoideae and Papilionoideae was 0%, 96%, 99% respectively. Conflicting reports on the nodulation status of some Caesalpiniod legumes have been discussed. Doubtful reports on nodulation may arise from inaccurate identification of root nodules. This is particularly due to the fact that structures like galls, tumors, knots, hypertrophies and mycorrhizae that grow on the roots bear superficial resemblance with nodules. It is interesting to note that major cases of doubtful nodulation reported in the past for Leguminosae concern Caesalpinioideae. The matter needs investigation at the molecular level. Present results confirm early findings that nodule formation is more commonly present than absent in Mimosoideae and Papilionoideae, the reverse is true for Caesalpinoideae.

Keywords: nodulated legumes, taxonomy, international database.

RESUMO - Os rizóbios são bactérias gram-negativas que infectam raízes de plantas leguminosas e formam nódulos radiculares. As simbioses entre leguminosas e rizóbios são de importância prática no fornecimento sustentável de alimentos e no aumento da produtividade agrícola. As listas existentes publicadas sobre a capacidade de nodulação das leguminosas paquistanesas foram mescladas para a compilação de uma lista abrangente. A lista continha 225 espécies, distribuídas em 75 gêneros que eram nativos do Paquistão. As leguminosas foram organizadas de acordo com as recomendações do Centro Internacional de Informações e Bases de Dados sobre Leguminosas (ILDIS) para espécies leguminosas do sul da Ásia. Das 225 espécies examinadas, 28 pertenciam à subfamília Caesalpinioideae; 29, à subfamília Mimosoideae; e 168, à superfamília Papilionoideae. A porcentagem de nodulação em Caesalpinioideae, Mimosoideae e Papilionoideae foi de 0%, 96% e 99%, respectivamente. Foram discutidos relatórios com dados conflitantes sobre o estado de nodulação de algumas leguminosas da subfamília Caesalpinioideae. Relatos imprecisos sobre nodulação podem surgir devido à identificação incorreta de nódulos radiculares. Isso ocorre especialmente porque estruturas como galhas, tumores, nós, hipertrofias e micorrizas, que crescem nas raízes, guardam alguma semelhança com os nódulos. É interessante notar que os

*** Corresponding author:**
<atariq@cdfa.ca.gov>

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[1] Department of Botany, University of Karachi, Karachi-75270, Pakistan; [2] California Department of Food and Agriculture, Sacramento. CA 95832, USA.

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principais casos de nodulação duvidosa relatados previamente para leguminosas dizem respeito à subfamília Caesalpinioideae. A questão precisa ser investigada em nível molecular. Os resultados atuais confirmam achados anteriores de que há maior presença do que ausência de formação de nódulos em Mimosoideae e Papilionoideae, e o inverso ocorre para Caesalpinoideae.

Palavras-chave: legumes com nódulos, taxonomia, base de dados internacional.

INTRODUCTION

Leguminosae is the third largest family of Angiosperms, with 16000-19000 species distributed in about 750 genera (Allen and Allen, 1981). Leguminous plants grow throughout the world but their greatest diversity is found in the tropics (Polhill and Raven, 1981). Many members of the group form nitrogen fixing symbiosis with root nodule rhizobia bacteria and other newly discovered non-rhizobial genera (Graham, 2008). Information on the occurrence of nodules in Leguminosae is very incomplete and even the comprehensive lists published (Allen and Allen, 1981; Halliday and Nakao, 1982; Faria et.al., 1989) contain no information on the nodulating ability of legumes growing in many parts of the world. The global records of nodulation compiled by Allen and Allen (1981) and Faria et al. (1989) indicate that only 15% and 20% of species have been examined, respectively. Since the publication of second global data (Faria et al., 1989), substantial data on nodulation in Leguminosae has accumulated (Moreira et al., 1992; Aguilar et al., 1994; Faria et al., 1994, 1998; Athar and Harding, 2000). A number of reports have also appeared and they describe the nodulation status of Pakistani legumes. These include Athar (1993, 1996, 1997, 2005), Athar and Mahmood (1990), Mahmood and Iqbal (1994), and Mahmood and Qadri (2004). The present paper presents a comprehensive list on the nodulating behavior of Pakistani legumes.

MATERIAL AND METHODS

Pakistan lies between 33°-40° N and 73°-10° E with a total area of 881,913 sq km (Ali and Qaiser, 1986). About 86% of the total area of Pakistan consists of arid lands (Quraishi et al., 1993). There is much diversity of terrain and temperature at any given time. Pakistan has a continental climate. Precipitation varies widely from less than 125 mm to over 1,500 mm per annum (Ali and Qaiser, 1986).

Legumes form a prominent and widespread part of flora of Pakistan, where 107 genera and 530 species have been reported (Ali, 1973a,b; 1977). Since 1977, many more legume genera and species from Pakistan have been identified. An account of these plants has been published in Legumes of South Asia: a Check-List (Kumar and Sane, 2003). Legume treatments in the book were used to compile a list of Pakistani legume genera, species, subspecies and varieties. One hundred ten (110) genera and 666 species were recorded. Extensive studies to examine root systems of leguminous plants for nodules have been conducted in Pakistan. Legumes were collected from all over Pakistan from diverse and geographically widely separated localities. Legumes examined for nodulation included both cultivated and wild or naturally occurring species ranging from small herbaceous weeds to woody shrubs and large trees. Plants were uprooted carefully not to damage or lose nodules on the root system and then examined with a hand lens.

Reports published on nodulation status of Pakistani legumes by Athar (1993, 1996, 1997, 2005), Athar and Mahmood (1978, 1980, 1985, 1990), Mahmood and Iqbal (1994) and Mahmood and Qadri (2004) were merged to compile a comprehensive list containing 75 genera and 225 species. The list was then compared with worldwide (Allen and Allen, 1981; Halliday and Nakao, 1982; Faria et al., 1989; Athar and Vasileva, 2013) reports on nodulation or non-nodulation. Results are shown in Table 1. The general taxonomy used here unless specified follows the one by Kumar and Sane (2003) where Leguminosae is divided into three subfamilies, Caesalpinioideae, Mimosoideae and Papilionoideae. The salient feature of the present contribution is that the taxa included in the Pakistani lists of nodulation/non nodulation but not described in Kumar and Sane (2003) have not been included in the current list.

RESULTS AND DISCUSSION

A consolidated account of the results of nodulation surveys carried out in Pakistan are presented in Table 1. Nodulation studies are not only the source of increasing database of nodulating or non-nodulating legumes throughout the world (Allen and Allen, 1981) but they also provide an indirect means of exploring new symbiotic nitrogen fixing associations operating in natural ecosystems (Rao, 2014). As a result, diverse groups of Gram-negative bacteria have been identified that are involved in forming nodules on the roots and sometimes on stems of leguminous plants (Graham, 2008). Nodule-forming bacteria are divided into 8 genera among Alpha-protobacteria: *Azorhizobium*, *Mesorhizobium*, *Methylobacterium*, *Rhizobium*, *Sinorhizobium* (Einsfer), *Devosia* and *Blastobacter* and 2 genera *(Burkholderia and Cupriavidus)* within betaprotobacteria (Zahran, 2009). There is plenty of evidence that *Burkholderia* forms nitrogen-fixing symbiosis with *Mimosa* spp. (Mimosoideae) and *Cyclopia* spp. (Elliot et al., 2007a) and *Rynchosia* spp. (Garau et al., 2009) – both members of Papilionoideae. *Cupriavidus taiwanensis* is also reported to form symbiosis with *Mimosa* spp. (Chen et al., 2001; Elliot et al., 2007b). Out of 110 genera and 666 legume species reported from Pakistan (Kumar and Sane, 2003), 14 genera and 59 species belonged to Caesalpinioideae, 14 genera and 58 species belonged to *Mimosoideae* and 82 genera and 549 species belonged to Papilionoideae. Out of 110 genera, 75 genera (68%) and out of 666 species, 225 species, (34%) have been examined for nodulation (Table 1). The table included four tribes of Caesalpinioideae, three tribes of Mimosoideae and 17 tribes of Papilionoideae. The four tribes of Caesalpinioideae included Caesalpineae, Cassieae, Cercideae and Detarieae. Together, they formed 9 genera and 28 species all of which were found to be non-nodulated (zero% nodulation). Factors contributing to non-nodulating behavior of Caesalpinioideae have been discussed by Allen and Allen (1976) and Sprent (2009).

Contradictory reports on the nodulation status of six Caesalpinioid legumes were found in Pakistani research reports on nodulation. Positive nodulation was found on the roots of *Delonix regia*, *Caesalpinia pulcherima*, *Cassia roxburgii*, *Tamarindus indicus* and *Senna occidentalis* (Athar and Mahmood, 1980) and *Senna holosericea* (Mahmood and Qadri, 2004). Faria et al. (1989) have researched and discussed the literature on the nodulation behavior of the genera *Caesalpinia*, *Cassia*, *Senna*, *Delonix* and *Tamarindus* and concluded that they were non-nodulated. In the light of this report, the nodule-like structures observed by Athar and Mahmood (1980) and Mahmood and Qadri (2004) were reinvestigated by Mahmood and Iqbal (1994) and Athar (2005), respectively. Smears and sections of doubtful structures were prepared and viewed under the microscope (Somasegaran and Hoben, 1994). The internal structure of these bodies did not conform to the internal structure of a legume nodule (Sprent and Sprent, 1990). These species have been included as non-nodulating in Table 1. Doubtful reports on nodulation may arise from inaccurate identification of root nodules. This is particularly due to the fact that structures like galls, tumors, knots, hypertrophies and mycorrhizae that grow on the roots have superficial resemblance with nodules (Faria et al., 1989). It should be noted that maximum cases of doubtful nodulation reported in the past for Leguminosae refer to Caesalpinioideae. The matter needs research at the molecular level. The study species of Mimosodeae belonged to the tribes Acacieae (12 species), Ingeae (9 species) and Mimoseae (8 species). Most of the nodulating species in Papilionoideae were distributed into the tribes Phaseoleae (35 species), Trifolieae (25 species), Viceae (21 species), Desmodieae (17 species), Indigofereae and Galeageae (12 species each), Crotolarieae (10 species), Genisteae (9 species), Milleteae (7 species), Robineae (5 species), Hedasereae (4 species), Dalbergieae and Sophoreae (3 species each), Aeschynomeneae (2 species), and Cicerae, Loteae and Thermopsoideae (one species each). The plants examined for nodulation that are members of the subfamily Papilionoideae were the largest group. Out of 225 species examined, 168 species belonged to Papilionoideae, 29 to Mimosoideae and 28 to Caesalpinioideae. Out of 168 species, 167 species of Papilionoideae except for *Ebnus stellata* and 28 out of 29 species of Mimosoideae except for *Adenanthera pavonina* were found to be nodulated, whereas all the 28 members of Caesalpinioideae were found to be non-nodulated. Absence of nodulation recorded in the Caesalpinioldeae of Pakistan is related to the non-occurrence of well-known nodulating tribes and genera from the flora of Pakistan (Ali in Kumar and Sane, 2003). The non-nodulating Caesalpinioid taxa have been figured out by Allen and Allen (1981) and Faria et al. (1989). The percentages of nodulation in Caesalpinoideae, Mimosoideae and Papilionoideae were 0%, 96%, and 99% respectively. These research findings are similar to the existing data on nodulation

summarized by Allen and Allen (1981), Faria et al. (1989, 1994), Mahmood and Iqbal (1994), Athar and Harding (2000) and Sprent (2009). The present results confirm early findings that nodule formation is more commonly present than absent in Mimosoideae and Papilionoideae, while the reverse is true for Caesalpinoideae.

Table 1 - Legume species examined for nodulation in Pakistan

Legume Species	Nodulation data
CAESALPINIOIDEAE	
CAESALPINEAE	
Caesalpenia bonduc (L.) Roxb.	–
C. gilliesii (Hook) D. Dieter.	–
C. pulcherrima (L.) Sw.*	–
Delonix elata (L.) Gamble.	–
D. regia (Hook) Raf. *	–
Parkinsonia aculeata L.	–
Peltophorum pterocarpum (DC) K. Heyne.	–
CASSIEAE	
Cassia fistula L.	–
C. roxburgii DC*	–
Senna alata (L.) Roxb.*	–
S. alexandrina Mill.	–
S. auriculata (L.) Roxb.	–
S. corymbosa (Lam.) H.S Irwin and Barneby.	–
S. holosericea (Fresen) Greuter*	–
S. italic Mill.	–
S. italica Mill. Subsp. *italica.*	–
S. italica subsp. *mirantha* (Brenen) Lock.	–
S. occidentalis (L.) Link.*	–
S. siamea (Lam.) H.S. Irwin & Barneby	–
S. sophera (L.) Roxb.	_
S. sophera (L.) var *purpurea* (Lindl.) V. Singh.	_
S. surrattensis (Burm. f.) H. S. Irwin & Barneby.	_
CERCIDEAE	
Bauhinia purpurea (L.)	–
B. racemosa Lam.	–
B. tomentosa L.	–
B. variegata L.	–
Cercis siliquastrum L.	–
DETARIEAE	
Tamarindus indica L.*	–
MIMOSOIDEAE	
ACACIEAE	
Acacia aneura Benth.	+
A. farnesiana (L.) Willd.	+
A. leucophloea (Roxb.) Willd.	+
A. modesta Wall.	+
A.nilotica (L.) Delile.	+
A. nilotica subsp. *hemispherica* Ali & Faruqi	+
A. nilotica subsp. *cupressiformis* (Stewart) Ali &Faruqi.	+
A. nilotica subsp. *indica* (Benth.) Brenan.	+
A nilotica subsp. *subalata* (Vatke.) Brenan.	+
A.saligna (Labill) H. Wendl.	+
A. senegal (L.) Willd.	+
Faidherbia albida (Delile) A. Chev.	+

Legume Species	Nodulation data
INGEAE	
Albizia chinensis (Osbeck) Merr.	+
A. julibrissin Durazz.	+
A. Julibrissin var *mollis* (Wall.) Benth.	+
A. lebbeck (L.) Benth.	+
A. odoratissma (L.f.) Benth.	+
A. procera (Roxb.) Benth.	+
Enterolobium contortisiliqum (Vell.) Morong.	+
Pithecellobium dulce (Roxb.) Benth.	+
Samanea saman (Jacq.) Merr.	+
MIMOSEAE	
Adenanthera pavonina L.	–
Leucaena leucocephala (Lam) de Wit.	+
Mimosa himalayana Gamble.	+
M. pudica L.	+
Prosopis cineraia (L) Druce.	+
P. farcata (Bank & Sol) J. F. Macbr.	+
P. glandulosa Torr.	+
P. juliflora (Sw) DC.	+
PAPILIONOIDEAE	
AESCHYNOMENEAE	
Aeschynomene indica L.	+
Arachis hypogea L.	+
CICERAE	
Cicer arietinum L.	+
CROTALARIEAE	
Crotolaria albida Roth.	+
C. burhia Benth.	+
C. Juncea L.	+
C. medicaginea Lam.	+
C. medicaginea Lam. var *medicaginea.*	+
C. prostrata Willd.	+
C. sessiflora L.	+
C. sessiflora L. subsp. *hazarensis* Ali.	+
C. sessiflora L. subsp. *sessiflora.*	+
C. spectabilis Roth.	+
DALBERGIEAE	
Dalbergia lanceolaria L.f.	+
D. latifolia Rox.	+
D. sissoo DC.	+
DESMODIEAE	
Alysicarpus bupleurifolius (L.) DC.	+
A. heterophyllus (Baker) Jafri & Ali	+
A. longifolius (Spreng) Wight & Arn.	+
A. monilifer (L.) DC.	+
A. ovalifolius (Schumach) J. Leonard.	+
A. rugosus (Willd) DC.	+
A. Scariosus (Spreng) Thwaites.	+

Legume Species	Nodulation data
DESMODIEAE	
A. tetragonolobus Edgew.	+
Camphylotropis meeboldii (Schindl) Schindil.	+
Codariocalyx motorius (Hoult) H. Ohashi.	+
Desmodium gangeticum (L.) DC.	+
D. laxiflorum DC.	+
D. podocarpum DC.	+
D. triflorum (L.) DC.	+
Lespedeza floribunda Bunge.	+
L. juncea (L.f) Pers.	+
Uraria picta (Jacq) DC.	+
GALEGEAE	
Alhagi maurorum Medik.	+
Astragalus amherstianus Benth.	+
A. leucocephalus Benth.	+
A. psilocentros Fisch.	+
A. subumbellatus Klotzch.	+
A. tribuloides Delile.	+
A. trichocarpus Benth.	+
Caragna ambigua Stocks,	+
Colutea nepalensis Sims.	+
Galega officinalis L.	+
Gueldenstaedtia verna (Georgi.) Boriss.	+
Oxytropis mollis Benth.	+
GENISTEAE	
Argyrolobium flaccidum (Royle) Jaub. & Spach.	+
A. roseum (Camb.) Jaub.& Spach.	+
A. roseum subsp *ornithopodiodes* (Jaub & Spach) Jafri & Ali	+
A. roseum (Camb.) Jaub.& Spach, subsp. *roseum.*	+
A. stenophylum Boiss.	+
Lupinus albus L.	+
L. pilosus L.	+
L. polyphyllus Lindl.	+
Spartium junceum L.	+
HEDYSAREAE	
Ebnus stellata Boiss.	–
Onobrychis cornuta (L.) Desv.	+
O. dealbata Stocks.	+
Tavernieria lappacea (Forssk) DC.	+
INDOGOFEREAE	
Cyamposis tetrogonoloba (L.) Taub.	+
Indigofera argentea Burm.	+
I. cordifolia Roth.	+
I. hebepetala Baker.	+
I. hebepetala var *glabra* Ali.	+
I. hebepetala (Benth.) Baker var *hebepetala*	+
I. himalayensis Ali.	+
I. hochstetteri Baker.	+
I. linifolia (L.f) Retz.	+
I. oblongifolia Forssk.	+
I. sessisliflora DC.	+
I. tinctotia L.	+
LOTEAE	
Lotus corniculatus Benth.	+
MILLETTIEAE	
Millettia pinnata (L.) Panigrahi.	+
Tephrosia purpusea (L.) Pers.	+
T. strigosa (Dalzell) Santapau & Mahesh.	+

Legume Species	Nodulation data
MILLETTIEAE	
T. subtriflora Baker	+
T. uniflora Pers.	+
T. villosa (L.) Pers.	+
Wisteria sinensis (Sims) Sweet.	+
PHASEOLEAE	
Cajanus cajan (L.) Millsp.	+
C. mollis (Benth.) Maesen.	+
C. platycarpus (Benth.) Maesen.	+
Canavalia africana Dunn.	+
Clitoria ternatea L.	+
Erythrina herbacea L.	+
E. suberosa Roxb.	+
Flemingia strobilifera (L.) W.T. Aiton.	+
F. strobilifera (L.) var *strobilifera.*	+
Glycine max (L.) Merr.	+
Lablab purpureus (L.) Sweet subsp *purpureus.*	+
L. purpureus (L.) Sweet subsp *bengalensis* (Jack) Verdec.	+
Macroptilum lathyroides (L.) Urban.	+
Mucuna nigricans (Lour.) Steud.	+
M. puriens (L.) DC.	+
Phaseolus coccineus L.	+
P. lunatus L.	+
P. vulgaris L.	+
Puraria lobata (Willd) Sanjappa & Pradeep.	+
P. tuberosa (Willd) DC.	+
Ryncosia minima (L.) DC.	+
R. pulverulenta Stocks.	+
R. pseudo-cajan Cambess.	+
R. rothii Aitch.	+
Vigna aconitifolia (Jacq.) Marecel.	+
V. dalzelliana (Kuntze.) Verdc.	+
V. mungo (L.) Hepper.	+
V. radiata (L.) Wilczek.	+
V. radiata (L.) Willcazek var. *radiata.*	+
V. radiata (L.) Willcz. var *setulosa* Ohwi & Ohashi.	+
V. trilobata (L.) Verdec.	+
V. umbellata (Thumb) Ohwi & Ohashi.	+
V. unguiculata (L.) Walp.	+
V. unguiculata subsp. *ungiculata* (L.) Walp.	+
V. unguiculata subsp *vexillata* (L.) A Rich.	+
ROBINEAE	
Robinia pseudoacacia L.	+
Sesbania bispinosa (Jacq.) W.F. Wight.	+
S. conclor J.B. Gillet.	+
S. grandiflora (L.) Poir.	+
S. sesban (L.) Merr.	+
SOPHOREAE	
Sophora alopecuroides L.	+
S. mollis (Royle) Baker	+
S.mollis (Royle) Baker subsp. *griffithii* (Stocks) Ali.	+
THERMOPSIDEAE	
Thermospis inflata Cambess.	+
TRIFOLIEAE	
Medicago edgeworthii Sirj.	+
M. falcata L.	+
M. laciniata (L.) Mill.	+
M. laciniata (L.) Mill var *lancinata.*	+

Legume Species	Nodulation data
TRIFOLIEAE	
M. lanciniata (L.) Mill var *brachycantha* Boiss.	+
M. lupulina L.	+
M. minima L.	+
M. monatha (C.A. Mey) Trautv.	+
M. polymorpha L.	+
M. Sativa L.	+
Melilotus albus Medik.	+
M. indicus (L.) All.	+
M. officinalis (L.) Pall.	+
Trifolium alexandrinum L.	+
T. dubium Sibth.	+
T. fragiferum L.	+
T. incarnatum L.	+
T. pretense L.	+
T. repense L.	+
T. resupinatum L.	+
Trigonella corniculata (L.) L.	+
T. emodi Benth.	+
T. foenum-graceum L.	+
T. gracilis Benth.	+
T. uncata Boiss & Noe	+
VICEAE	
Lathyrus aphaca L.	+
L. emodi (Fritsch) Ali.	+
L. hirsutus L.	+
L. humulis (Ser.) Spreng.	+
L. latifolius L.	+
L. odoratus L.	+
L. pratensis L.	+
L. sativus L.	+
L. sphaericus Retz.	+
Lens culinaris Medik.	+
Pisum sativum (L.)	+
Vicia bakeri Ali	+
V. benthamiana Ali.	+
V. faba (L.)	+
V. hirsuta (L.) S.F Gray.	+
V. monantha Retz. Subsp. *Monantha*	+
V. perigrina L.	+
V. rigidula Royle.	+
V. sativa L.	+
V. sepium L.	+
V. tenuifolia Roth.	+

+ indicates nodules present, - denotes nodules absent.

* indicates doubtful nodulation.

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