

**Long-distance Dispersal: The Case for the Allopolyploid  
*Glycine tabacina* (Labill.) Benth. and *G. tomentella*  
Hayata in the West-Central Pacific.**

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**Abstract**—Fourteen diploid ( $2n = 40$ ) perennial species in the genus *Glycine* Willd. subgenus *Glycine* are endemic to the Australian region. However, the allopolyploid cytotypes ( $2n = 80$ ) of *G. tabacina* (Labill.) Benth. and *G. tomentella* Hayata have a wider distribution. The allopolyploid members of *G. tabacina* are found in Australia and on islands in the South and West-Central Pacific. Similarly, the allopolyploid members of *G. tomentella* occur in the Australian region and in the West-Central Pacific. Most probably, migratory birds are the dissemination vector for the allopolyploid members of *G. tabacina* and *G. tomentella* across the equator from the Australian region to the West-Central Pacific.

### Introduction

The genus *Glycine* Willd. is composed of two subgenera, *Glycine* and *Soja* (Moench) F. J. Herm. (Table 1). The subgenus *Soja* includes the cultivated soybean, *G. max* (L.) Merr. and its wild ancestor, *G. soja*. Sieb. and Zucc. Both species are annual and diploid with 40 chromosomes (Singh & Hymowitz 1988). The soybean, domesticated in the eastern half of North China, is found only under cultivation while *G. soja* occurs in the People's Republic of China, the U.S.S.R., Taiwan, Japan, and peninsular Korea.

The subgenus *Glycine* currently contains fifteen inbreeding wild perennial species (Table 1). The diploids ( $2n = 40$ ) are restricted in distribution to the Australian region. *Glycine tabacina* (Labill.) Benth. contains both diploid ( $2n = 40$ ) and tetraploid ( $2n = 80$ ) members (Table 1). The diploid forms of *G. tabacina* are found only in Australia. On the other hand, the tetraploid members of *G. tabacina* have a wide distribution. They occur in the Pescadores Archipelago, the islands of Quemoy and Amoy just off the coast of Fujian Province, People's Republic of China, Ryukyu Islands (Japan), and the Mariana Islands in the West-Central Pacific (Table 2). The tetraploid forms of *G. tabacina* also are found in Australia and in the South Pacific islands of New Caledonia, Vanuatu, Fiji, Tonga and Niue.

*Glycine tomentella* Hayata is composed of four cytotypes:  $2n = 38, 40, 78,$  and  $80$  (Table 1). The 38-chromosome form only is found in Australia. The 40- and 78-

Table 1. The species in the genus *Glycine* Willd., somatic chromosome number, genome symbols and distribution.<sup>1</sup>

Species	2n	Genome symbol	Distribution
Subgenus <i>Glycine</i>			
<i>G. albicans</i> Tind. and Craven	40	—	Australia
<i>G. arenaria</i> Tind.	40	—	Australia
<i>G. argyrea</i> Tind.	40	A <sub>2</sub> A <sub>2</sub>	Australia
<i>G. canescens</i> F. J. Herm.	40	AA	Australia
<i>G. clandestina</i> Wendl.	40	A <sub>1</sub> A <sub>1</sub>	Australia
<i>G. curvata</i> Tind.	40	—	Australia
<i>G. cyrtoloba</i> Tind.	40	CC	Australia
<i>G. falcata</i> Benth.	40	FF	Australia
<i>G. hirticaulis</i> Tind. and Craven	80	—	Australia
<i>G. lactovirens</i> Tind. and Craven	40	—	Australia
<i>G. latifolia</i> (Benth.) Newell and Hymowitz	40	B <sub>1</sub> B <sub>1</sub>	Australia
<i>G. latrobeana</i> (Meissn.) Benth.	40	—	Australia
<i>G. microphylla</i> (Benth.) Tind.	40	BB	Australia
<i>G. tabacina</i> (Labill.) Benth.	40	B <sub>2</sub> B <sub>2</sub>	Australia
	80	AAB <sub>2</sub> B <sub>2</sub> or BBB <sub>2</sub> B <sub>2</sub>	Australia, West Central and South Pacific Islands
<i>G. tomentella</i> Hayata	38	EE	Australia
	40	DD	Australia, Papua New Guinea
	78	DDEE	Australia, Papua New Guinea
	80	AADD	Australia, Papua New Guinea, Philippines, Taiwan
Subgenus <i>Soja</i> (Moench) F. J. Herm.			
<i>G. soja</i> Sieb. and Zucc.	40	GG	P.R.C., U.S.S.R., Taiwan, Japan, Korea
<i>G. max</i> (L.) Merr.	40	GG	Cultigen

<sup>1</sup> Adapted from Singh and Hymowitz 1985a, Singh *et al.* 1988, 1989, Tindale & Craven 1988.

chromosome forms occur both in Australia and in nearby Papua New Guinea. The tetraploid forms of *G. tomentella* ( $2n = 80$ ) occur in Australia, Papua New Guinea, the Philippines and Taiwan (Table 3).

Phylogenetic relationships among the wild perennial *Glycine* species have been established based on crossability, hybrid viability and meiotic chromosome pairing in intra- and inter-specific hybrids (Doyle *et al.* 1986, Grant *et al.* 1984a, 1984b, 1986, Newell & Hymowitz 1983, Palmer & Hadley 1968, Putievsky & Broué 1979, Singh & Hymowitz 1985a, 1985b, Singh *et al.* 1987, 1988). Genome symbols have been assigned to 9 of the 15 wild perennial species by Singh & Hymowitz (1985a) and Singh *et al.* (1988) (Table 1).

The complexes of *G. tabacina* ( $2n = 40, 80$ ) and *G. tomentella* ( $2n = 38, 40, 78, 80$ ) evolved through allopolyploidization (Singh *et al.* 1987, 1989). The 80-chromosome forms of *G. tabacina* are composed of two distinct morphological complexes having one common diploid parent: with (BBB<sub>2</sub>B<sub>2</sub>) and without (AAB<sub>2</sub>B<sub>2</sub>) adventitious roots

(Table 1) (Costanza & Hymowitz 1987, Singh *et al.* 1987). Both 80-chromosome forms of *G. tabacina* have been found in Australia and West-Central Pacific. The allotetraploid forms of *G. tomentella* on Taiwan have similar genomes (AADD) to those of their counterpart *G. tomentella* found in Queensland, Australia (Singh *et al.* 1987).

In the past decade extensive plant exploration trips were undertaken in the West-Central Pacific seeking *Glycine* but no diploid perennial *Glycine* species were located (Tables 2, 3). Thus the question arises concerning the origin of the allopolyploid forms of both *G. tabacina* and *G. tomentella* in the West-Central Pacific. The distribution of the

Table 2. University of Illinois (IL) accessions of *Glycine tabacina* from the west-central Pacific, location and somatic chromosome number. Voucher specimens are deposited in the herbarium of the Crop Evolution Laboratory (CEL), University of Illinois, Urbana.

Accession number	Plant introduction number	Origin	2n
325	319697	Quemoy Is., Taiwan	80
326	320545	Penghu Is., Pescadores, Taiwan	80
329-2	320546	Taichung, Taiwan	80
330	320549	Quemoy Is., Taiwan	80
381	393533	Ie Is., Ryukyu, Japan <sup>1</sup>	80
382	393534	Miyako Is., Ryukyu, Japan <sup>1</sup>	80
582	446972	Ie Is., Ryukyu, Japan <sup>2</sup>	80
583	446973	Ie Is., Ryukyu, Japan <sup>2</sup>	80
584	446974	Miyako Is., Ryukyu, Japan <sup>2</sup>	80
585	446975	Miyako Is., Ryukyu, Japan <sup>2</sup>	80
586	446976	Kurima Is., Ryukyu, Japan <sup>2</sup>	80
587	446977	Shimaji Is., Ryukyu, Japan <sup>2</sup>	80
588	446978	Shimaji Is., Ryukyu, Japan <sup>2</sup>	80
589	446979	Ishigaki Is., Ryukyu, Japan <sup>2</sup>	80
624	483198	Tinian Is., Marianas <sup>3</sup>	80
625	483199	Tinian Is., Marianas <sup>3</sup>	80
626	483200	Saipan Is., Marianas <sup>3</sup>	80
870	—	Ishigaki Is., Ryukyu, Japan <sup>4</sup>	—
875	—	Penghu Is., Pescadores, Taiwan <sup>5</sup>	80
876	—	Paisha Is., Pescadores, Taiwan <sup>5</sup>	—
877	—	Hsiaomen Is., Pescadores, Taiwan <sup>5</sup>	—
878	—	Hsiyu Is., Pescadores, Taiwan <sup>5</sup>	—
879	—	Hsiyu Is., Pescadores, Taiwan <sup>5</sup>	—
880	—	Penghu Is., Pescadores, Taiwan <sup>5</sup>	—
881	—	Chumei Is., Pescadores, Taiwan <sup>5</sup>	—
882	—	Chumei Is., Pescadores, Taiwan <sup>5</sup>	—
883	—	Chumei Is., Pescadores, Taiwan <sup>5</sup>	—
884	—	Ghebay Is., Pescadores, Taiwan <sup>5</sup>	—

<sup>1</sup> Collected by M. Anagaki, Faculty of Agriculture, Ryukyu University, Naha, Japan.

<sup>2</sup> Collected by P. Broué, CSIRO, Div. of Plant Industry, Canberra, Australia.

<sup>3</sup> Collected by C. A. Newell, Dept. of Agronomy, Univ. of Illinois, Urbana, IL.

<sup>4</sup> Collected by M. S. Yeh, National Chung-Hsing University, Taichung, Taiwan.

<sup>5</sup> Collected by T. Hymowitz, Dept. of Agronomy, Univ. of Illinois, Urbana, IL.

Table 3. University of Illinois (IL) accessions of *Glycine tomentella* from the west-central Pacific, location and somatic chromosome number. Voucher specimens are deposited in the herbarium of the Crop Evolution Laboratory (CEL), University of Illinois, Urbana.

Accession number	Plant introduction number	Origin	2n
352	233051	Hengchung, Taiwan	—
353	245332	unknown	80
356	320547	Quemoy Is., Taiwan	80
357	320548	unknown	80
360	330961	Batan Is., Philippines <sup>1</sup>	80
361	339655	Taichung Is., Taiwan <sup>2</sup>	80
383	393556	Maopitou, Taiwan <sup>3</sup>	80
384	393557	Maopitou, Taiwan <sup>3</sup>	80
385	393558	Maopitou, Taiwan <sup>3</sup>	—
528	441012	Maopitou, Taiwan <sup>4</sup>	80
529	441013	Maopitou, Taiwan <sup>4</sup>	80
871	—	Maopitou, Taiwan <sup>4</sup>	80
872	—	Ta Kuang, Taiwan <sup>4</sup>	—
873	—	Paisha, Taiwan <sup>4</sup>	80
874	—	Haikou, Taiwan <sup>4</sup>	—

<sup>1</sup> Collected by J. V. Pancho, Dept. of Botany, Univ. of the Philippines, Laguna, Philippines.

<sup>2</sup> Collected by Y. C. Lu, National Chung-Hsing University, Taichung, Taiwan.

<sup>3</sup> Collected by R. L. Bernard, USDA/ARS, Urbana, IL.

<sup>4</sup> Collected by T. Hymowitz, Dept. of Agronomy, Univ. of Illinois, Urbana, IL.

*Glycine* polyploid complexes, which are disjunct between Australia and the West-Central Pacific regions, requires an explanation.

### Characteristics of Seeds of the Subgenus *Glycine* Relevant to Dispersal

Seeds of the subgenus *Glycine* are black, dark brown or greenish with a smooth shiny, roughened muriculate or foveolate surface (Newell & Hymowitz 1978b). The seed weight varies from 0.4 to 1.6 grams per 100 seeds (Hymowitz *et al.* 1972). The seeds are short-oblong, suborbicular, oblong, ovoid-oblong, ovoid, and quadrate often truncate at the ends. The seeds are 1.5–4.0 mm long and 1.25–3.0 mm broad. To germinate the small, hard seeds in the greenhouse they must be scarified before planting. There are from 3 to 9 seeds per pod depending on the species. The pods are linear, short oblong or oval, reflexed or falcate. For information about a specific species, see Hermann 1962, Newell & Hymowitz 1980, Tindale 1984, 1986a, 1986b, Tindale & Craven 1988.

### Possible Explanations for the Disjunct Distribution

*Sea or air currents, rafting, animal or human dissemination.*

Wild perennial *Glycine* seed do not float on sea water nor do they possess any mechanism for long distance dispersal by air currents. Rafting on flotsam from Australia is pos-

sible, but highly unlikely as the small seed during rough weather conditions would wash off flotsam and sink. Neither the seed nor pods contain any special structures for adhering to coats of animals. Although humans colonized and regularly navigated among Pacific islands since prehistoric times (Lewis 1973), direct human transport northward from Australia nearly to Japan via island-hopping is unlikely because the literature makes no mention of uses by humans of wild perennial *Glycine* species.

#### *Plate tectonics and biogeography.*

After the breakup of Pangaea, the universal land mass, Australia, New Zealand and Antarctica were united with South America and with India-Madagascar-Africa, forming Gondwanaland (100 m.y. BP), a Southern Hemisphere land mass. The West-Central Pacific is associated with Laurasia, a Northern Hemisphere land mass.

New Zealand and New Caledonia separated from Australia and Antarctica about 80 m.y. BP and moved north-eastward reaching their present position about 60 m.y. BP. Australia and Antarctica separated about 49 m.y. BP. As Australia moved northward it entered a zone of reduced precipitation and increased aridity. The Australian plate collided with the Asian plate 10 to 12 m.y. BP. Most probably during this epoch, Miocene, some legumes entered Australia directly from Asia. At that time, Australia was widely separated from South America, India, Madagascar and Africa (Raven 1979, Raven & Axelrod 1972, Raven & Polhill 1981).

According to Lackey (1977, p. 85) both “the subgenus *Glycine* and the subgenus *Soja* are probably derived from *Pueraria*-like ancestors in tropical Asia. From this tropical center, species in the subgenus *Glycine* have successfully invaded Australia and associated areas, and the wild form in the subgenus *Soja* has invaded central and northern Asia.” *Glycine* species ( $2n = 40$ ) are diploidized polyploids (Hymowitz *et al.* in press, Kumar & Hymowitz 1989) with  $x = 10$ .

Singh *et al.* (1989) demonstrated that allopolyploidization of *Glycine* species ( $2n = 80$ ) took place in Australia. *Glycine canescens* ( $2n = 40$ , genome AA) was crossed to *G. tomentella* ( $2n = 40$ , genome DD). The chromosomes of the  $F_1$  plant (genomes AD) were doubled using colchicine. The amphiploid plant (genomes AADD) was hybridized with *G. tomentella* from Queensland. The progeny were fertile and the chromosomes paired normally. Since *G. canescens* is not found in the West-Central Pacific, South Pacific nor on Papua New Guinea, the only place where allopolyploidization could have taken place is Australia. Thus, perennial *Glycine* found a niche in tropical and subtropical Australia. Radiation of *Glycine* species, followed by allopolyploidization of the species, resulted in the *G. tabacina* and *G. tomentella* species complexes.

As mentioned in a previous section, there are no reports of diploid perennial *Glycine* species in the West-Central Pacific nor in all of Asia or Africa. If the assumption were made that perennial tetraploid forms of *G. tabacina* and *G. tomentella* represent relict populations in the West-Central Pacific of once broadly distributed Asia perennial *Glycine* populations, that assumption would be difficult to reconcile based upon recent genome affinity studies. Both perennial tetraploid *G. tabacina* forms (with and without adventitious roots) and tetraploid *G. tomentella* from the West-Central Pacific produce fertile  $F_1$  hybrids when crossed with their counterparts from Australia (Singh *et al.* 1987). Thus, the genomes making up the allopolyploid complexes would have had to be maintained and

conserved similarly in differing environments for a long period of time for the *Glycine* relict population assumption to be valid. This is possible, but highly unlikely. Hence, neither plate tectonics nor relict populations can be used to explain the present disjunct distribution patterns between the tetraploid perennial *Glycine* species in the West-Central Pacific and Australia.

*Long-distance dispersal of seed by birds.*

Long-distance dispersal of seed by birds has been well documented (Carlquist 1974). Birds that feed in *Glycine* habitats can transport seeds by ingestion accidentally (including inside the stomachs of ingested prey, Grant *et al.* 1975) or as a nutrient. They and birds that merely walk in *Glycine* habitats or in aquatic areas that drain *Glycine* habitats may pick up the small, light seeds in mud adhering to their feet.

Candidates for dispersal agents include species whose breeding ranges include Australia and also islands near Asia (some Columbiformes, Apodiformes), individuals of which therefore cross the equator often enough to maintain migration in the genetic sense. They also include migrants, both those that winter in Australia and breed in the West-Central Pacific and those that pass through the West-Central Pacific enroute to breeding grounds in East Asia, Siberia, or Alaska (e.g. Charadriiformes). In addition, cosmopolitan species such as some Laridae are known to transport seeds (Gillham 1956).

According to Williams & Williams (1988) the study of actual migration paths of birds from Asia to Australia and the South Pacific is in its infancy. They cite a number of reports concerning the movement of shore-birds between East Asia and Micronesia, Australia and New Zealand. The investigators conducted radar and visual observations of southward shore-bird migration on Guam and concluded a significant number of birds passed over the island enroute to the western Pacific Ocean, however without stopping on Guam.

McClure (1974) reported that banding studies revealed that the migratory range of the Wandering Tattler (*Heteroscelus* [*Tringa*] *incanus*) was from Moreton Bay, Queensland to Magadan, eastern Siberia, U.S.S.R. passing through Chiba, Japan. Moreton Bay is situated near the southern border of Queensland close to New South Wales. Curiously, both allopolyploid forms of *G. tomentella* and *G. tabacina* are found in the general region. Another bird, Latham's Snipe (*Lymnocyptes* [*Capella*] *hardwickii*), based again on banding studies, had a range from northern Japan to near Sydney Australia.

Shorebirds (Charadriiformes) are the most promising candidates for agents of *Glycine* transport because of their documented migrations and their documented retention of seeds. Therefore, we concentrate on this group as a likely but not necessarily the only agent of transport.

Seeds are retained for long periods in shorebirds. Proctor (1968) and de Vlaming & Proctor (1968) have demonstrated that a wide variety of seeds, especially those larger than 1 mm and having a hard seedcoat may be retained in the digestive tract in Killdeer (*Charadrius vociferus*) and Least Sandpipers (*Erolia minutilla*) for more than 100 hours and then excreted in a viable form. *Glycine* seeds have these characteristics. With flight speeds relative to the air of 30–60 km hr<sup>-1</sup> (Greenwalt 1975) and nonstop migrations across thousands of kilometers, shorebirds can transport seeds the required distances.

Do birds selectively ingest or walk in habitats containing tetraploid *Glycine* cyto-

types? There is no evidence that diploid *Glycine* seeds are not carried by birds. However, the allopolyploid forms of *G. tabacina* and *G. tomentella*, unlike their diploid counterparts, are aggressive colonizing species (Singh & Hymowitz 1985b). Thus, the tetraploid plants may be able to compete successfully and establish themselves in the West-Central Pacific while the diploids are unsuccessful.

In conclusion, cytogenetic studies on allopolyploid forms of *G. tabacina* and *G. tomentella* all recently collected in the West-Central Pacific region reveal that they are genomically similar to allopolyploid forms of *G. tabacina* and *G. tomentella* found in Australia. Allopolyploidization of these species took place in Australia. Therefore the West-Central Pacific allopolyploid *Glycine* species originated in the Australian region. A likely, indeed the only available, agent for the hypothesized long-distance transport of *Glycine* seeds across the equator is transport by migratory birds.

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