AMPHICARPIC LEGUMES FOR TROPICAL PASTURE PERSISTENCE

R. Schultze-Kraft, A. Schmidt and H. Hohn
Institute of Plant Production in the Tropics and Subtropics
University of Hohenheim (380), D-70593 Stuttgart, Germany

ABSTRACT

Amphicarpy, by which a plant produces underground seeds in addition to aerial fruits, is found in many plant families and in species of at least 15 legume genera. First studies on the tropical *Centrosema rotundifolium* and subtropical *Macroptilium panduratum* revealed for both species, besides their stoloniferous growth habit, two important mechanisms for survival under unfavorable conditions: (1) Underground meristems and reserve organs, and (2) regeneration from a soil seed reserve based on underground, aerial-flowering independent, seed production. Underground seed production was for both species particularly high on very sandy soils, but amphicarpy enables the plants to exhibit a plasticity response to unfavourable soil conditions by changing resource allocation from underground to above-ground reproduction. The latter, which seems to be influenced by cross-pollination and thus aids gene-recombination, favours spreading of plant populations whereas underground reproduction ensures population survival on-site. Preliminary information on the agronomic potential of both species is given and several research needs are highlighted.

KEYWORDS

Tropical pastures, legumes, *Centrosema rotundifolium*, *Macroptilium panduratum*, amphicarpy, underground reproduction, persistence, plasticity

INTRODUCTION

The potential impact of tropical pasture legumes on livestock production is limited by a series of constraints, among them the lack of legume persistence in mixture with grasses and under grazing. Legume persistence is not only influenced by grazing mismanagement and other environmental stresses but also by the inherent regeneration ability of the plant. There are several important regeneration/persistence mechanisms, among them (1) stoloniferous growth habit, (2) low-lying or underground meristems and reserve organs, and (3) formation of a soil seedbank. Studies of herbarium sheets suggest that several regeneration-relevant characteristics can be found in amphicarpic legumes. In this paper the role of amphicarpy for plant persistence and the potential of two tropical amphicarpic legumes are described and discussed.

Amphicarpy. Amphicarpy is a specialized form of dimorphism found in a number of plant species where on the same individual, in addition to aerial fruits, some of the fruits/seeds are produced below the soil surface on underground peduncles. These peduncles develop from the nodes of trailing stems right into the soil where they branch out and produce a large number of cleistogamous, subterranean flower buds and eventually fruits. First described in 1601, amphicarpy is a phylogenetically young and very variable phenomenon which so far has only been studied by botanists and ecologists (Cheplick, 1987). It is known to occur in as many as 17 plant families, among them in 15 tropical, subtropical and temperate genera of the Leguminosae, predominantly in the Phaseoleae and Vicieae tribes (Table 1).

The species

Origin and description. The species selected for further studies of their amphicarpy and agronomic potential are *Centrosema rotundifolium* and *Macroptilium panduratum*. The former is mainly native to the semiarid and dry-subhumid tropics of Brazil (Schultze-Kraft et al., 1990), the latter to the semiarid tropics and subtropics of Brazil, Paraguay and Argentina (Barbosa-Fevereiro, 1986). Both occur on very sandy soils, are stoloniferous, and have a trailing growth habit. Both develop strong, tuberous roots, not only on the seed-borne mother plant but also on stolon-borne, adventitious plants. In both species, most underground pods are found in the first 15 cm topsoil layer.

***Centrosema rotundifolium*: Performance and seed production.** This species is adapted to light-textured, acid and low-fertility Oxisols where herbage yields, however, are rather modest. The nutritive value (16-29% crude protein content; 44-71% *in vitro* dry-matter digestibility; phosphorus and calcium contents of 0.15-0.79 % and 0.31-1.07%, respectively) is intermediate to high (Schultze-Kraft et al., 1994; Schmidt et al., 1996). *C. rotundifolium* forage is palatable to grazing cattle. In the Colombian Llanos Orientales, the underground reproductive phase began simultaneously with the above-ground reproductive phase; it seems to be favoured by grazing or cutting. Aerial seed production seems to depend on tripping of flowers by insects (Schmidt et al., 1996). Seed yields can be very high on sandy soils: In eastern Venezuela, a destructive harvest of six *C. rotundifolium* accessions yielded between 920 and 1900 kg of underground seed (in pod)/ha; seed yields from aerial pods were 13-856 kg/ha (I. Rodríguez, pers. comm.). Underground pods are mostly one-seeded. From seeds buried as deep as 30 cm, still 19% seedling emergence has been measured (Schmidt et al., 1996). *C. rotundifolium* shows good regrowth after burning.

***Macroptilium panduratum*: Performance**. *M. panduratum* is lesser known agronomically and has so far only been tested in the Chaco region of subtropical Paraguay. Its dry-matter (DM) production potential is high on sandy soils. According to preliminary data, the nutritive value is intermediate to high (16-22% CP, 6.8-7.7 MJ metabolizable energy/kg DM, 0.27-0.41% P), but palatability to cattle is apparently low. The above-ground reproductive phase started 3-4 weeks earlier than underground. Underground pods contain 1-4 seeds but are predominantly two-seeded. Segregating aerial-flower colors can occasionally be observed and suggest the occurrence of allogamy. In their upper portion, the tuberous roots bear meristems that enable new regrowth after destruction of above-soil biomass.

Soil influence on amphicarpy. Both species exhibit a clear tendency towards increased production of underground reproductive structures on sandy soils; this is shown in Figure 1 for *M. panduratum*. For *C. rotundifolium,* two years after completion of a non-destructive field experiment, 180.4 seeds/m^2 were counted as soil seed reserve on a very sandy soil (60% sand) in comparison with 24.4 seeds/m^2 on a loamy soil (20% sand). On the heavier soil, aerial seed production and formation of tuberous roots are favoured at the expense of underground seed production; this was particularly evident in *C. rotundifolium*.

CONCLUSIONS AND RESEARCH NEEDS

Conclusion. Through amphicarpy, both species can ensure (1) persistence of a population via underground seed, and (2) gene-recombination via aerial flowering and spreading through above-ground seeds. Amphicarpy furthermore enables the plants to adapt to different environmental conditions by changing the allocation of resources from underground to above-ground reproduction and viceversa ("plasticity"). Both legumes have the potential of a three-fold persistence strategy: Stoloniferous growth habit, underground meristems and reserve organs, and continuous replenishment of the soil seed reserve. The latter seems to be insofar particularly important as underground seed production is not affected by removal (e.g., consumption by grazing livestock) of aerial biomass. Both species seem to have a particular potential for very sandy soils. If and when *C. rotundifolium* and *M. panduratum* do not prove suitable for direct use, they may be valuable donors of amphicarpy genes for plant breeding programs in other, commercially important, *Centrosema* and/or *Macroptilium* species.

Research needs. Among important future-research topics are: (1) broadening the genetic base of available germplasm through further collection in the wild (for example, recently an unexpected, subtropical *C. rotundifolium* form, which differs very much from the common tropical type, was found by A. Glatzle in the Paraguayan Chaco); (2) examination and evaluation of other amphicarpic legumes such as *C. grazielae*, *M. gracile* and *Vigna* spp.; (3) influence of grazing and/or cutting management on underground seed production, legume persistence in mixture with grasses, and animal production; and (4) testing the species' potential for non-forage uses such as sand dune stabilization.

REFERENCES

Barbosa-Fevereiro, V.P. 1986. *Macroptilium* (Bentham) Urban do Brasil (Leguminosae-Faboideae-Phaseoleae-Phaseolinae). Arq. Jard. Bot. Rio de J. **28**: 109-180.

Cheplik, G.P. 1987**.** The ecology of amphicarpic plants. Trends Ecol. Evol. **2**(4)**:** 97-101.

Schmidt, A., R. Schultze-Kraft, B.L. Maass and R. Herrmann. 1996. Aspects of the amphicarpy of the tropical pasture legume *Centrosema rotundifolium* Mart. ex Bentham. Proc. Third Int. Herb. Seed Conf., Halle, Germany, pp. 44-48.

Schultze-Kraft, R., R.J. Williams and L. Coradin. 1990. Biogeography of *Centrosema*. Pages 29-76 *in* R. Schultze-Kraft and R.J. Clements, eds. *Centrosema*: Biology, Agronomy, and Utilization. CIAT, Cali, Colombia.

Schultze-Kraft, R., G. Keller-Grein, E. Cárdenas and F. Díaz Bolívar. 1994. Potencial de *Centrosema rotundifolium* como leguminosa forrajera. Past. Trop. **16**(3): 2-8.

Figure 1
Underground peduncle production of *Macroptilium panduratum* on two contrasting soils in the Paraguayan Chaco.

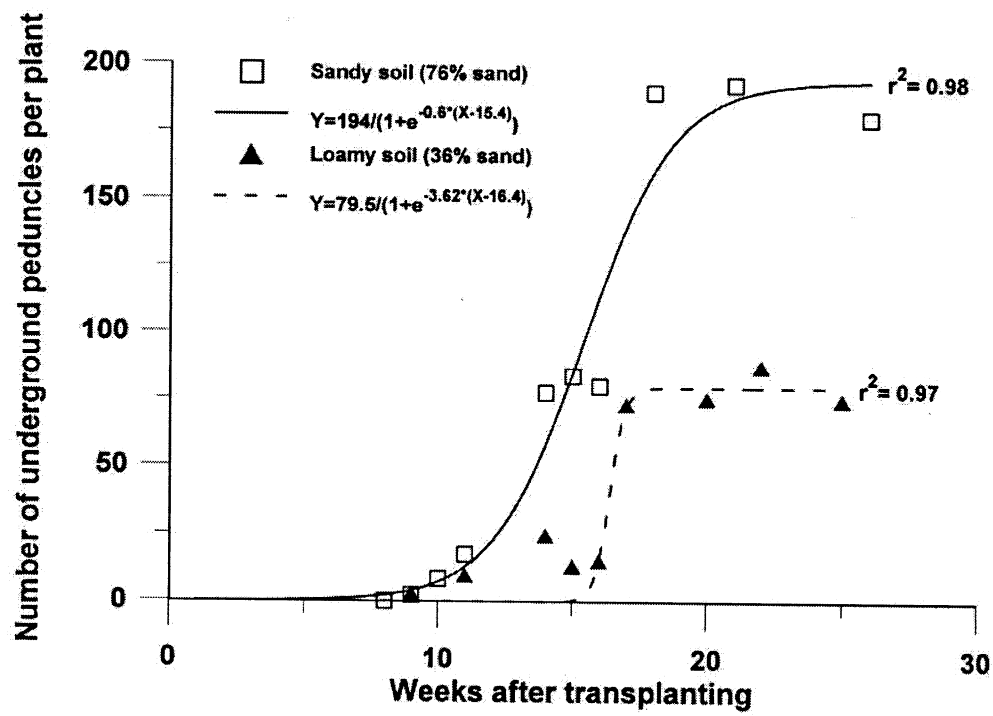

Table 1
Occurrence of amphicarpy in legume genera and tribes, and in species of *Centrosema* and *Macroptilium*

Amphicarpaea (Phaseoleae)	*Lathyrus* (Vicieae)	*Pisum* (Vicieae)
Centrosema (Phaseoleae)	*Macroptilium* (Phaseoleae)	*Tephrosia* (Tephrosieae)
Clitoria (Phaseoleae)	*Neocracca* (Robinieae)	*Trifolium* (Trifolieae)
Galacti (Phaseoleae)	*Orobus* (Vicieae)	*Vicia* (Vicieae)
Glycine (Phaseoleae)	*Phaseolus* (Phaseoleae)	*Vigna* (Phaseoleae)

Centrosema spp.:	*Macroptilium* spp.:
C. bracteosum Benth.	*M. gracile* (Poepp. ex Benth.) Urban
C. grazielae Barbosa	*M. heterophyllum* (Willd.) Maréchal et Baudet
C. heptaphyllum Moric.	*M. panduratum* (Mart. ex Benth.) Maréchal et Baudet
C. rotundifolium Mart. ex Benth.	*M. pedatum* (Rose) Maréchal et Baudet
C. venosum Mart. ex Benth.	