Gynodioecy in *Teucrium racemosum* (Lamiaceae)

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Introduction

When describing *Teucrium albicaule* Toelken, the author drew attention to its gynodioecy and intimated that some 'atypical' specimens of *T. racemosum* R.Br may represent male-sterile plants of that species (Toelken 1985). While collecting in remnant native vegetation of the lower Avoca Plain between Kerang and Quambatook in May 2012, we observed extensive clonal populations of a small-flowered *Teucrium* L. in general habit like *T. racemosum*, typical forms of which were common and also extensively clonal in the area. The staminal filaments of the small-flowered plants were barely longer than the corolla tube while those of typical *T. racemosum* are much longer than the corolla tube (Figs 1, 2). The habitat at the site is an extensive grassland/low shrubland developed on red clay, ranging from hard-setting compact clay to self-mulching/cracking clay. Topography is generally flat, but shallow gilgais and puffs are present. Annual rainfall is approximately 350 mm.

Results and discussion

The small-flowered plants conformed to what had been described as Teucrium racemosum var. polymorphum Tovey & P.Morris (1922). Alternatively, such plants had been suggested by Conn (1999) to be hybrids between T. racemosum and T. albicaule. However, T. albicaule is a very rare species in the lower Avoca Plain area and its nearest occurrence is about 10 km from the small-flowered population of *T. racemosum*. At this site, T. albicaule is near its most easterly known occurrence in Victoria, and at least 100 km from the next known occurrence. Apart from the small flowers, there are no traits of these populations that suggest any parental contribution from T. albicaule, although apparent genuine hybrids between these two species are known from further north and west of the Kerang area. The leaves of the small-flowered plants are undivided and elliptic-ovate rather than trifoliolate with linear leaflets, and are generally significantly longer than the upper limit (10 mm) ascribed to *T. albicaule*. A simpler explanation for these small-flowered plants is that *T. racemosum*, like *T. albicaule* is also gynodioecious, according with Toelken's (1985)

Abstract

Clonal populations of small-flowered plants of *Teucrium racemosum* R.Br from north-western Victoria were examined, and gynodioecy suggested as the simplest explanation for their form and distribution. *Teucrium racemosum* var. *polymorphum* Tovey & P.Morris and *T. racemosum* var. *triflorum* J.M.Black are consequently placed in synonymy under *T. racemosum*.

Key words: male-sterile, clonal populations, grassland

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suggestion, but apparently not confirmed in this species before. Examination of *T. racemosum* specimens at MEL revealed plants of this flower type also occur in Western Australia, Northern Territory and New South Wales (see below, and e.g. Conn 2012, Figs 1 & 2). It is possible that similar plants are to be found through the entire range of *T. racemosum*. The main floral differences between the hermaphroditic and female forms are summarised in Table 1.

Close inspection found anthers of the small-flowered form to be empty or with only small amounts of relatively small pollen grains (av. $30.4 \pm 1.7 \times 29.5 \pm 0.4$ microns, Fig. 3), including many misshapen grains. This supports the notion that these are female plants, or at least have a reduced male function. Hermaphroditic flowers from the same area had abundant, normal-appearing pollen (av. $44.6 \pm 2.3 \times 47.1 \pm 1.7$ microns, Fig. 4). It was noticed in the field (and evident on herbarium collections made from these plants) that the small-flowered plants were relatively prolific in

producing fruit. A cursory inspection of the sympatric large-flowered (and presumably hermaphrodite) plants detected none of these to be forming fruit, although examination of *T. racemosum* specimens at MEL shows that fruits are produced by large-flowered plants also. Despite the comment by Cunningham et al. (1992) that plants of 'var. polymorphum' (i.e. those plants here believed to be female) produced fewer mericarps, our collections showed that the plants typically matured all four mericarps per flower. We assume that seed production is a consequence of pollen being transferred from hermaphroditic to female plants, but the possibility of apomixis cannot be discounted without further investigation. Apomixis has been reported in Thymus loscosii Willk. (Orellana et al. 2005), another gynodioecious member of the Lamiaceae.

Observations across the Riverina over many seasons by one of us (EOB) suggest there is normally little overlap in flowering times of the two forms, with the male-sterile form typically flowering in cooler seasons (autumn and



Figure 1. Small-flowered (female) form of *Teucrium racemosum* (= var. *polymorphum*) from the lower Avoca Plain (*N.G. Walsh* 7557 & E. O'Brien (MEL))



Figure 2. Typical, hermaphroditic *Teucrium racemosum* sympatric with the female form shown in Fig. 1 (*N.G. Walsh* 7558 & E. O'Brien (MEL))

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spring) while the large-flowered form typically flowers during summer, particularly following summer rain. The unusually wet summer/early autumn of 2012 appears to have prolonged flowering of the large-flowered form resulting in a considerable period of overlap in anthesis of the two flower types. There is also an interesting observed difference in the distribution of both forms in relation to soil type, with the male-sterile form almost exclusively inhabiting hard-setting (infrequently cracking) clay/clay-loam, and the hermaphrodites on the softer, self-mulching clays and loams. This soil type preference may help explain the observed difference in peak flowering times between the male-sterile and hermaphrodites as the different soil types respond very differently to seasonal rainfall events.

Genetic studies on *Arabidopsis thalliana* (L.) Heynh. (Brassicaceae) have shown that a gene linked to pistil development is negatively associated with corolla development (Weigel & Meyerowitz 1993) suggesting a reason why female flowers commonly have smaller

corollas than hermaphroditic flowers of the same species (Delph 1996). It is a possible explanation for the floral pattern displayed by *Teucrium racemosum*.

It would appear from herbarium collections held at MEL that male-sterile plants are relatively uncommon. Only five specimens (including the type of var. *polymorphum*) were of this form amongst 294 specimens from all Australian mainland states at MEL (non-flowering specimens however were not determinable as to flower type). However, observations through the Riverina area of New South Wales and Victoria (*sensu* IBRA 2012) indicate that both forms are common in grasslands. Perhaps the smaller-flowered plants are overlooked or avoided by collectors on the assumption that flowers are simply not yet fully formed.

Gynodioecy is relatively common in Lamiaceae, and members of this family were among the first plants to be studied by Charles Darwin when he first described this phenomenon (Darwin 1877). It has generally been believed that gynodioecy is derived from the

Table 1. Summary of major noral differences between nermaphrodutic and female reacham racemosum			

	Hermaphrodites	Females
Pedicel length (mm)	8–18	2–6
Calyx length (mm)	4.5–6	2.5–4.5
Corolla dorsal lobe length (mm)	3–5	1.5–2
Corolla median ventral lobe length (mm)	6–12	3–5
Filament length (mm)	9–11	1.5–3.5
Style length (mm)	10–13	4–5

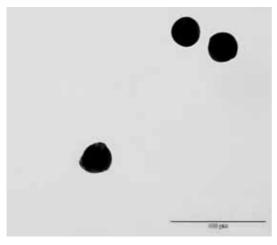


Figure 3. Pollen of small-flowered (female) form of *Teucrium* racemosum stained in Methylene Blue (scale bar = $100 \mu m$; from N.G. Walsh 7557 & E. O'Brien (MEL))

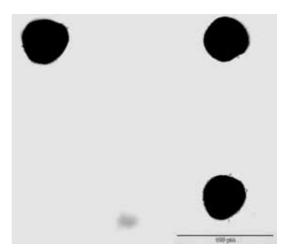


Figure 4. Pollen of hermaphroditic *Teucrium racemosum* stained in Methylene Blue (scale bar = 100 μm; (from N.G. Walsh 7558 & E. O'Brien (MEL))

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hermaphroditic state, rather than being derived from, or giving rise to dioecy (e.g. Lewis 1942). However, Ross (1978) proposed mechanisms whereby gynodioecy may be transitional toward dioecy from the conventional hermaphroditic condition, albeit via more complex genetic processes.

Several studies across a wide range of families suggest that the female plants may compensate for the absence of male function by possessing traits that, for example, increase floral longevity (Petterson 1992), reduce likelihood of inbreeding depression (Lloyd 1975; Charlesworth & Charlesworth 1987) or elevate levels of seed production (Lewis 1941; Lloyd 1976). Observation suggests that the latter trait is being expressed at the Avoca Plain site at least.

Taxonomy

Teucrium racemosum R.Br. *Prodr.* 504 (1810)

Type: **SOUTH AUSTRALIA.** Spencers Gulf, 1802, *R. Brown* (holo: BM; iso: CANB).

Teucrium racemosum var. polymorphum Tovey & P.Morris, Proc. Roy. Soc. Victoria new ser. **35**, 89 (1922). Type: Victoria. Kerang, Sept. 1920, E.J. Semmens (holo: MEL!).

Teucrium racemosum var. triflorum J.M. Black, Fl. South Australia 3: 486 (1926). Type: South Australia: Eringa near Lindsay Creek, 3.X.1913, White s.n. (holo: AD, photo seen).

Teucrium sp. B. sensu Jacobs, S.W.L. & Pickard, J. (1981), Plants of New South Wales, fide Conn (2012),

Specimens seen: ('var. polymorphum' form = female-flowered plants): WESTERN AUSTRALIA. (Geraldton Sandplains, sensu IBRA 2012) 10 mile (16.1 km) peg along main road to Kalbarri from North West Coastal Highway, December 1918, E. Officer 9/19 (CANB, MEL, NSW). NORTHERN TERRITORY. (Finke, sensu IBRA 2012) Jimmys Dam, 23 km ESE Erldunda Homestead, 26.vi.2000, P.K. Latz 16361 (MEL, NT). NEW SOUTH WALES. (Nandewar, sensu IBRA 2012) Red Bobs Reserve, c. 40 km SW of Gunnedah, 30.i.2005, J.R. Hosking 2580 (CANB, MEL, NE, NSW). VICTORIA. (Riverina, sensu IBRA 2012) Kerang, Victoria, September 1920, E.J. Semmens 72 (MEL – type of var. polymorphum); 26.5 km due W from Kerang, 29.iv.2012, N.G. Walsh 7557, J.P. Walsh & E. O'Brien (AD, CANB, MEL, PAL); (Murray Darling Depression) 17.9 km SW of Birchip, 5.x.2011, M.Argall s.n. (MEL).

Note: Cunningham *et al.* (1992) report occurrences in south-western New South Wales in the Hay, Wanganella and Jerilderie districts, all within the Riverina region (*sensu* IBRA 2012).

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References

- Charlesworth, D. and Charlesworth, B. (1987). Inbreeding depression and its evolutionary consequences. *Annual Review of Ecology and Systematics* **18**, 237–268.
- Conn, B.J. (1999). 'Teucrium' in N.G. Walsh and T.J. Entwisle (eds), Flora of Victoria 4, pp. 456–459. Inkata Press: Port Melbourne.
- Conn, B.J. (2012). *Teucrium racemosum* in PlantNET The Plant Information Network System of The Royal Botanic Gardens and Domain Trust: Sydney, Australia (version 2.0, accessed 20.vi.2012). http://plantnet.rbgsyd.nsw.gov.au
- Cunningham, G.M., Mulham, W.E., Milthorpe, P.L. and Leigh, J.H. (1992). *Plants of Western New South Wales*. Inkata Press: Port Melbourne.
- Darwin, C.R. (1877). The different forms of flowers on plants of the same species, ed. J. Murray. University of Chicago Press: London.
- Delph, L.F. (1996). 'Flower size dimorphism in plants with unisexual flowers', in D.G. Lloyd and S.C.H. Barrett (eds), *Floral biology: studies on floral evolution in animal-pollinated plants*, pp. 217–237. Chapman and Hall: York.
- IBRA (2012) Interim Biogeographic Regionalisation for Australia (version 6.1, accessed 20.vi.2012). http://www.environment. gov.au/parks/nrs/science/bioregion-framework/ibra/index. html
- Lewis, D. (1941). Male sterility in natural populations of hermaphroditic plants. *New Phytologist* **40**, 56–63.
- Lewis, D. (1942). The evolution of sex in flowering plants. *Biological Reviews* **17**, 46–67.
- Lloyd, D.G. (1975). The maintenance of gynodioecy and androdioecy in angiosperms. *Genetica* **45**, 325–339.
- Lloyd, D.G. (1976). The transmission of genes via pollen and ovules in gynodioecious angiosperms. *Theoretical Population Biology* **9**, 299–316.
- Orellana, M.R., Blanché, C. and Bosch, M. (2005). Pollination and reproductive success in the gynodioecious endemic *Thymus loscosii* (Lamiaceae). *Canadian Journal of Botany* **83**, 183–193.
- Petterson, M.W. (1992). Advantages of being a specialist female in gynodioecious *Silene vulgaris* S.L. (Caryophyllaceae). *American Journal of Botany* **79**, 1389–1395.
- Ross, M.D. (1978). The evolution of gynodioecy and subdioecy. *Evolution* **32**, 174–188.
- Toelken, H.R. (1985). Notes on *Teucrium* L. (Labiatae). *Journal of the Adelaide Botanic Garden* **7**, 295–300.
- Tovey, J.R. and Morris, P.F. (1922). Contributions from the National Herbarium of Victoria 2. *Proceedings of the Royal Society of Victoria* n.s. **35**, 89.
- Weigel, D. and Meyerowitz, E.M. (1993). Activation of floral homeotic genes in *Arabidopsis*. *Science* **261**, 1723–1727.

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