

Are female and male flowers separated on different individuals in *Pseudopanax*?

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INTRODUCTION

An unusually high proportion of New Zealand's flowering plants are thought to be dioecious (Webb et al. 1999). A dioecious species has individuals that are either male (bearing only stamens) or female (bearing only ovules). Dioecy is different from cosexuality, where all individuals are hermaphrodite. In some cosexual plants, stamens and ovules may be borne in separate flowers but these both occur on the same hermaphrodite individual; this is monoecy. In others, the flowers all bear both stamens and ovules, usually termed hermaphroditism. Intermediates between, and variations on, these three main themes exist. For instance, in gynodioecy some male plants have flowers that are hermaphrodite and set low number of fruits. In andromonoecy, individual flowers are either male or hermaphrodite.

The lancewood and five-finger genus *Pseudopanax* is widely regarded as dioecious, although an historical account is complicated by changes in generic limits. We presently regard *Pseudopanax* as endemic to New Zealand, with twelve species (Perrie & Shepherd 2010), alongside the recognition of *Raukaua* (Mitchell et al. 1997).

Allan (1961) placed species now in *Pseudopanax* and *Raukaua* in *Pseudopanax* and *Neopanax* (there is not a one-to-one correspondence). He described his *Pseudopanax* as dioecious and *Neopanax* as dioecious or monoecious. However, in the treatments of the individual species, monoecy was only explicitly indicated for *Neopanax simplex* (now *Raukaua simplex*). Philipson (1965) stated that the species are “dioecious or, rarely, monoecious”, although it is unclear whether he was referring to a broadly defined *Pseudopanax* or only to the species included by Allan (1961) in *Neopanax*. Moore & Irwin (1978) illustrated separate male and female flowers for *P. arboreus*, suggesting that it was either monoecious or dioecious. For *P. crassifolius*, they illustrated a male flower and a “bisexual (functionally female?) flower”, but implied that there were separate female

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individuals (e.g., dioecy or gynodioecy). Webb et al. (1999), in a review of gender dimorphism in the New Zealand flora, listed *Pseudopanax* as dioecious, but noted that the “genus includes species or populations that are cosexual” (cosexuality includes monoecy and hermaphroditism). They did not provide further details, and referenced only Allan (1961). Metcalf (2000) stated that “the flowers are dioecious” for *Pseudopanax* (with a circumscription encompassing *Raukaua*). Eagle (2006) recognised both *Pseudopanax* and *Raukaua*, and stated *Pseudopanax* to be dioecious. She drew separate male and female flowers for a number of species (including *P. lessonii*), but noted that the flowers of the individual of *P. ferox* she illustrated were bisexual.

We have collected numerous *Pseudopanax* specimens for our research projects (Perrie & Shepherd 2009, 2010), especially *P. crassifolius*, *P. crassifolius* × *P. lessonii*, *P. ferox*, and *P. lessonii*. During our field-work, it has been difficult to reconcile our observations of *Pseudopanax* flowers with the categorisation of the genus as dioecious. This is because we are yet to note an individual of the above taxa that was flowering and not exhibiting male characteristics. All flowering individuals appear to have at least some flowers that are clearly male (i.e., they have normal-looking stamens). Fruiting individuals are common, and obviously indicate female function. But, if these species are dioecious, where are the individuals that produce only female flowers?

Because of our doubts about the breeding system of *Pseudopanax*, we followed the flower development of a cultivated plant of *P. lessonii*.

METHODS

A small, potted plant of *Pseudopanax lessonii* was bought from Oratia Nursery, Auckland. At the time of purchase, the sample was producing many flower buds (but none were open); it had presumably been regenerated from a cutting of adult material. The sample was sold as the Surville Cliffs ‘variant’ of *P. lessonii*. Its tri-foliolate (three-leaflets) morphology is consistent with this.

We kept the sample on the porch of our Palmerston North home, and monitored its flowering during 2009. The same ray within a multi-rayed umbel was photographed to record phases of flower development. Flowering commenced late February, and observations continued until mid-October. Our monitored sample was the only flowering *Pseudopanax* within at least a hundred metre radius (our house is largely surrounded by pasture, and the only other *Pseudopanax* we have are non-flowering juveniles).

Some umbels were bagged in muslin curtain mesh to investigate the effect of excluding animal pollinators.

RESULTS

The flower development of our *Pseudopanax lessonii* sample is illustrated in Fig. 1. The basal flowers within umbel rays opened first, and those at the apex last. At opening, the flowers clearly exhibited male reproductive organs. The stamens were well formed, and pollen was evident in the anthers. The male phase for each flower was short-lived, with the stamens and petals being shed within one or two days of the flower opening. On the umbel ray that was photographically tracked, all ten flowers had shed their stamens and petals just ten days after the first flowers had opened. Both flies and ants were observed visiting the flowers (Fig. 2).

On the tracked umbel ray, the basal whorl of flowers did not develop further, and eventually abscised. Swelling of the ovary was evident in the apical whorl of flowers after a month, suggesting fertilisation and fruit development. The fruit slowly enlarged and changed from green to purplish-black (Fig. 1). One of the fruits was larger than the others from an early stage; it eventually became mottled with white, possibly indicating that it was 'ripe' (see Fig. 3). These patterns (i.e., abscission of the basal flowers; coloration and size changes; uneven development of the fruit; few fruit reaching 'ripeness', <20%) were common to other umbel rays. Tracking of fruit development was ended by an October storm that destroyed most of the rays/umbels, including the one that was being photographed.

White-mottled (ripe?) fruit from umbel rays other than the one being tracked were dissected and found to contain five seeds. Seeds also appeared to be present in fruit that were small and dark coloured (unripe?). They were likely less developed, but this was not confirmed.

The effect of the muslin bags on pollination was not clear, in large part because they induced a higher rate of umbel mortality. This was probably because of the weight of the bags, and their catching of the wind. In the bagged umbels that did survive for an appreciable time, fruit development did appear to occur, but it may have been stunted compared to the non-bagged umbels. Although the muslin bags probably prevented visitation by flying insects, ants easily breached them (the bags were apparently not secured sufficiently tightly around the base of the umbel).

DISCUSSION

Our sample of *Pseudopanax lessonii* appears to have hermaphrodite flowers. Flowers that had normal-looking and pollen-producing anthers eventually developed into fruit containing seeds. Caveats to this conclusion are that the functionality of the pollen and seeds were not explicitly tested. However, if our plant was functionally female only, it had rather well-developed

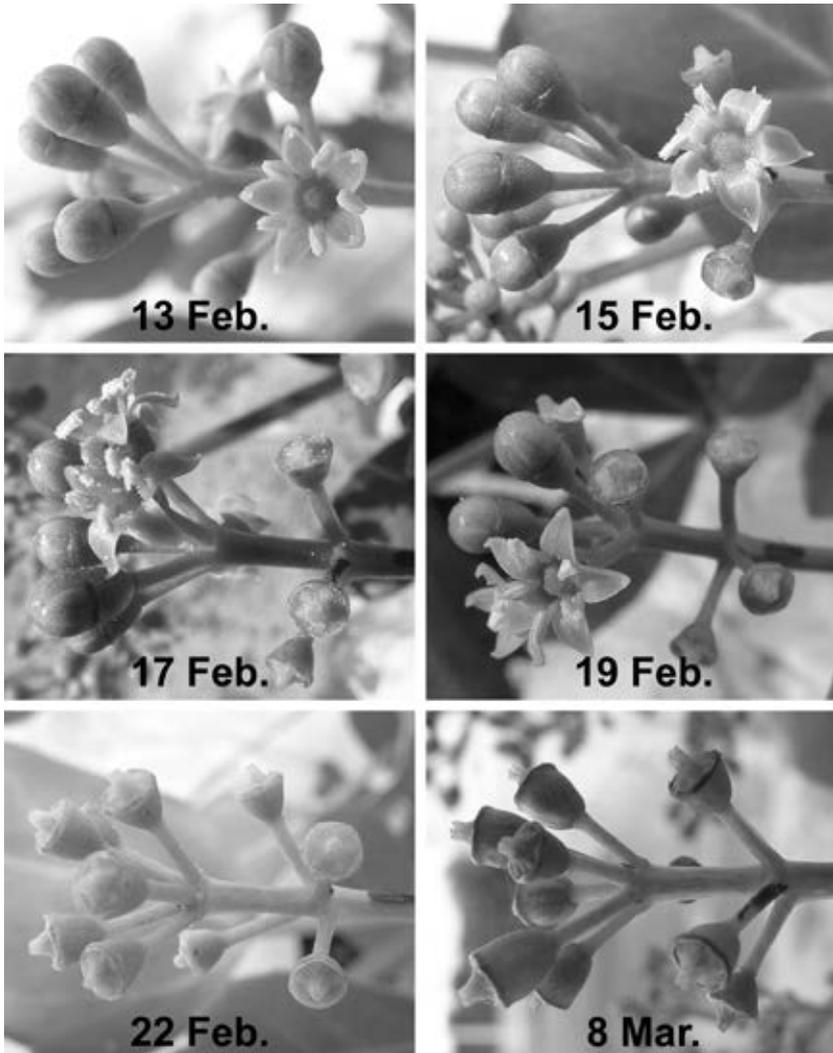


Figure 1. Progressive development of the flowers and fruit of one particular umbel-ray on our *Pseudopanax lessonii* sample.

stamens instead of them being reduced to staminodes (sterile structures that resemble stamens) or absent altogether; if our plant was functionally male only, it put a lot of effort into producing fruit-like structures.

Our tracked sample of *Pseudopanax lessonii* had only a few fruit progress to what appeared to be a ripe state, even after nearly eight months. These fruit are presumably the result of self-pollination (or apomixis), because of



Figure 1 (continued). Progressive development of the flowers and fruit of one particular umbel-ray on our *Pseudopanax lessonii* sample.

the absence of other flowering *Pseudopanax* individuals nearby. This selfing may have contributed to the low rate of fruit development on our sample, and, because *Pseudopanax* individuals generally set a lot of fruit, it would be interesting to compare via experiment the rate of fruit development between self- and out-crossed pollen.



Figure 2. Potential pollinators—a fly (left; 22 Feb.) and an ant (right; 23 Feb.) on flowers of our *Pseudopanax lessonii* sample.



Figure 3. The white mottling of the lower left fruit may indicate that it is (or is becoming) ripe. Note that this is a different umbel to that photographed in Fig. 1.

Hermaphroditism of the flowers of our tracked *Pseudopanax lessonii* sample accords with our field observations of *P. lessonii* (both Surville Cliffs and ‘typical’ plants), *P. crassifolius*, *P. crassifolius* × *P. lessonii*, and *P. ferox*. Rather than being dioecious, we suggest that these taxa predominantly bear hermaphrodite flowers, and this is probably also the case for the other lancewood and exstipulate five-fingers (see Perrie & Shepherd 2010). Whether flower

hermaphroditism is constant or variable is unknown. (Perhaps some flowers are male only; perhaps some populations are dioecious). Detailed assessment beyond our one tracked sample would be useful. Of the stipulate five-fingers, preliminary field observations of *P. arboreus* suggest it may well be dioecious.

We are uncertain when the hermaphrodite flowers are receptive to pollination. To avoid self-fertilisation within a flower, receptivity generally follows stamen abscission (see Merrett 2005a). It is interesting that resource allocation for fruit development appeared to be directed towards the apical flowers, and that the basal flowers abscised. If female function does follow male function within a flower, then the apical flowers may be more likely to be fertilised by pollen from different individuals (if within a population), as the earlier-opening basal flowers would have already shed their stamens (also see Jesson et al. 2006).

It is possible that the abscising basal flowers are actually functionally male rather than hermaphrodite. This would then be a case of andromonoecy, a common condition in Apiaceae and Araliaceae, and considered ancestral in Araliaceae by Schlessman et al. (2001). Evolution of dioecy from cosexuality via andromonoecy has been described as a pathway by Webb (1979, 1999), who cited *Aralia* as an example.

Our results are similar to those reported recently by Merrett (2005a) for *Raukaua anomalus*. Both *Pseudopanax* and *Raukaua* are in the Araliaceae family, although they are only distantly related (Mitchell et al. 1997). Like *Pseudopanax*, *Raukaua* was thought to be dioecious (or monoecious) (Merrett 2005a). However, Merrett (2005a) found *R. anomalus* to have flowers that were hermaphroditic and protandrous (the anthers mature before the stigmas become receptive). In *R. anomalus*, the male stage lasts for 36–48 hours, after which the stamens and petals completely abscise. The stigma then becomes receptive. The flowers are borne in clusters, and a cluster can comprise buds, flowers, and fruit at the same time. Merrett (2005a) stated that the prior erroneous interpretation of the breeding system of *R. anomalus* was probably because of the smallness of the flowers and the complete abscission of the stamens and petals after the male phase.

Our results and those of Braggins et al. (1999), Merrett (2005a,b), Garnock-Jones et al. (2007), and Gardner (2008) indicate there is still plenty to discover about even such basic aspects of our native plants as their breeding systems. Fortunately, profitable observations can be made even within one's own garden.

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