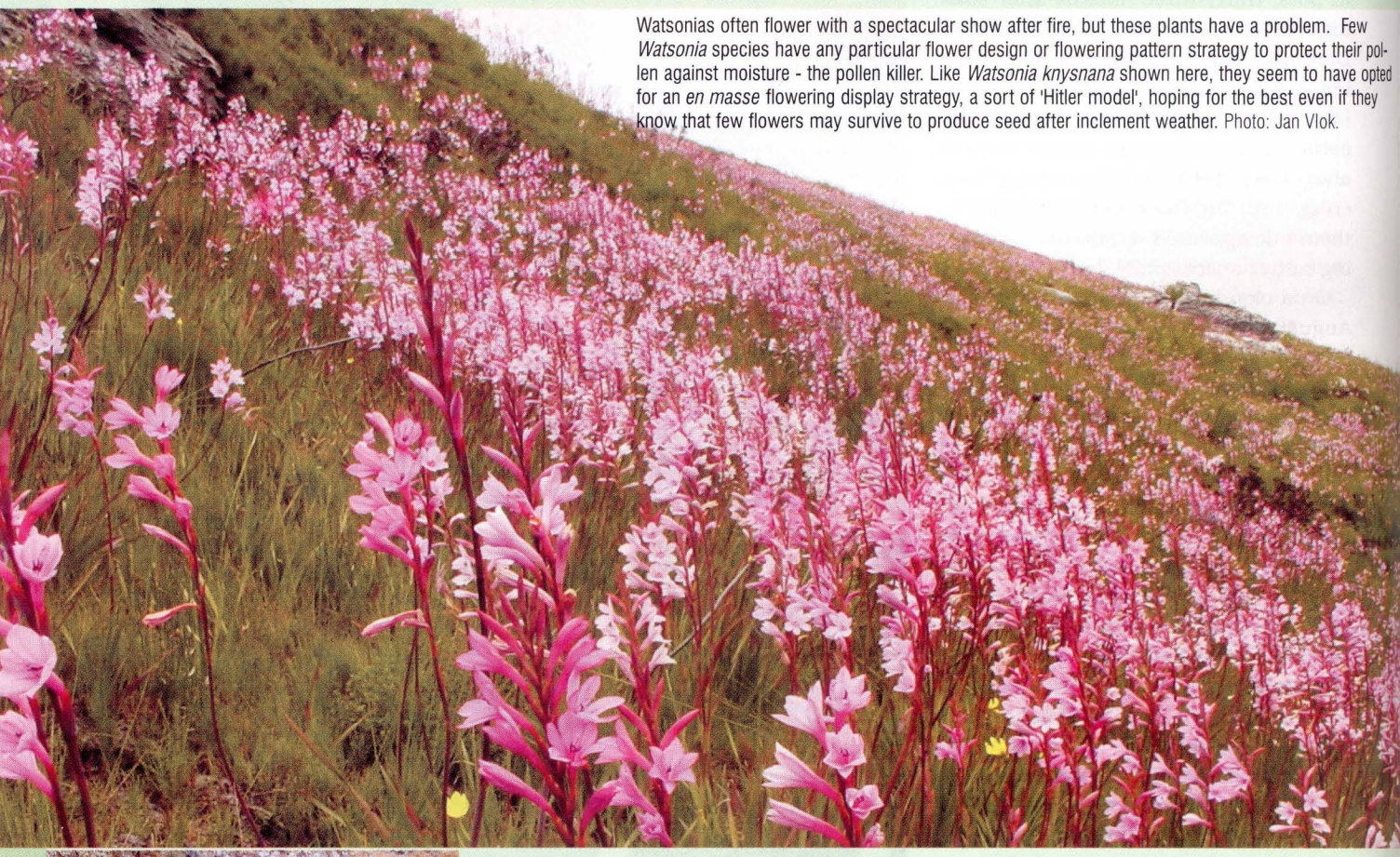
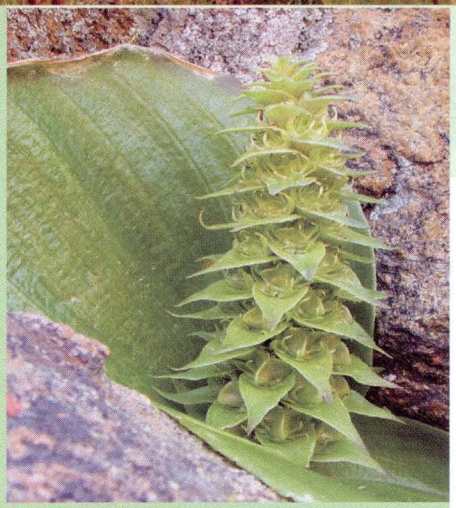
Why do some flowers close at night...



Watsonias often flower with a spectacular show after fire, but these plants have a problem. Few *Watsonia* species have any particular flower design or flowering pattern strategy to protect their pollen against moisture - the pollen killer. Like *Watsonia knysnana* shown here, they seem to have opted for an *en masse* flowering display strategy, a sort of 'Hitler model', hoping for the best even if they know that few flowers may survive to produce seed after inclement weather. Photo: Jan Vlok.

while others stay open until all hours, come rain or shine?

Jan Vlok looks at some intriguing examples of flower behaviour.



ABOVE: *Whiteheadia bifolia* employs a rather clever pagoda-like design to channel any rainwater away from the open flowers. A similar design also occurs in some *Eucomis* species. Photo: Jan Vlok.

While walking in the veld with Richard Cowling some time ago he asked me why I think some flowers close at night. My answer at the time was, 'to protect their pollen', based on the simple fact that the pollen of most plant species loses its viability when it gets wet. So closing your petals to protect your pollen from night dew - and on cool rainy days- makes good sense as a lack of viable pollen will nullify the entire reason for flowering.

But there is more to the story than my initial simple answer. Ever since Richard asked me that question I have been looking more carefully at flower behaviour and I would like you to join me to do just that. Flower behaviour? Yes, just like animals, plants also have a distinctive behaviour. They may not behave as individuals, but different species certainly behave differently in terms of their flowers. The flowers of some species remain open day and night, in others they only open during the warmer parts of a day, whereas some species only open at night. You all knew that, but think carefully about these three behavioral patterns again. Why do plants behave differently?

So, why do some flowers close in the evening and when it is cool during the day? A point clearly made in some recent articles in *Veld & Flora* indicated that certain plants only open their flowers when it is warm. The implication here is that plants get a signal as soon as the temperature drops in the evening, or when it remains cool during the day, that moisture is on its way. As soon as the temperature drops

in the evening the relative humidity of the air increases, or rain may be imminent if it remains cool during the day. So cool air indicates to plants that there is a risk that their pollen may become moist and it is best to close shop to prevent damage to goods. A second reason for closing shop is because no customers are on the street. The activity of most diurnal insects decreases at low temperatures, which for flowers means no clients - so just stay in bed all day and don't waste your energy. Just the opposite happens with nocturnal insects though. If, as a plant, you opt for nightlife clients, the evening signal to open your shop comes at a risk. The risk is losing the male function (production and storage of pollen in the stamen) of your flower: little point in having many pretty girls around in the evening without having some viable boys around. Several of our plants use this seemingly risky nightlife option, like the aandblommetjies (*Hesperantha* species). It is quite obvious why these plants open their flowers in the evening: to attract specific pollinators, but not very clear how they protect their pollen assets in the process, when other flowers tuck them up safe and dry. There is clearly more to the story than just the obvious.

Wash out

The first time I noted how moisture can affect pollination in plants was in a spectacular stand of *Watsonia fourcadei* flowers on the slopes of the Outeniqua mountains. I tried to collect pollen from these plants a day after rain, but could not find any, even though the flowers were perfectly intact. The rain washed away all the pollen that was released before the rain and none of the anthers of the other open flowers were willing to release their pollen: they were waiting for warmer weather. No pollen was thus available in this population for two to three days. Being puzzled by this I then marked the sections on the inflorescences that had open flowers with bits of wool and returned a few weeks later. Almost none of the flowers that were open at the time of the rain had developed capsules with viable seed, simply because there was no viable pollen to be pollinated. I have noted this subsequently many times in *Watsonia* and *Aloe* inflorescences. Once the plants are in seed one can even often tell when a cold front passed through the area, as a series of undeveloped capsules mark those rainy days. I suspect that the same happens in *Protea* flowers.

I recently saw another interesting example in my garden when I opened my sprinkler system to water a lovely bed of flowering *Nerine filifolia*. Not a single one of them produced seed afterwards, as I unthinkingly washed all the viable pollen away.

So we do have some species in which the flowers seem to offer little protection to protect their pollen from cool, wet conditions. These species seem to be characterized by inflorescences that produce many flowers that open sequentially over a prolonged period. So, those flowers that are literally caught with their pants down in wet conditions are simply compensated for by others that will open during better conditions.

Staying dry

By now some of you will probably already mumble that this is just another 'old-wives tale' with no scientific evi-

LEFT: *Aloe ferox,* like most other aloes, never closes its flowers. None, or very few, of these open flowers will set seed if it rains. Aloes often flower in the dry season but even if it rains, they just rapidly open a whole set of new flowers after the rain, and some will be pollinated. Once the plants are in seed one can even often tell that a cold front passed through, as a series of undeveloped capsules mark those rainy days.
Photo: Jan Vlok.

TOP RIGHT: Safety in numbers. *Protea pudens* is an example of a plant that does not seem to employ special measures to protect its pollen from getting wet. The inflorescence, however, consists of many flowers that are opened sequentially to ensure that new pollen is released after the rain has passed.

BELOW RIGHT: *Gladiolus rogersii* is a classic example of a 'windsock-flower', where a thin flexible flowering stem enables the flower to turn its back on any moisture-laden wind. This flower design often occurs in plants of high rainfall areas, where it allows the flowers to stay open at night or even when it rains because the pollen is very well protected against moisture.
Photos: Jan Vlok.

LEFT: Most of the carrion flowers, like this *Piaranthus comptus,* stay open at night and even when it rains. Like orchids, they have little to worry about as the viability of their pollen is safe: well protected in waterproof bags.
Photo: Jan Vlok.

dence. Well there is a way to test if flowers close when it cools down to protect their pollen from becoming wet. We can do this by comparing the flower behavior of species that have 'waterproof' pollen types with those that do not. The predicted outcome being that those species that do protect their pollen in 'waterproof' bags, or any other specific design of the anthers, would not close at night. Perhaps the best examples of plants that retain their pollen in waterproof bags are orchids and carrion-flowers (stapeliads). Thus far I have not seen any of our local orchids or stapeliads close their flowers at night or during inclement weather. Once open, they remain open even though many of them have only diurnal pollinators.

Another group of interesting plants that we can use to test the idea are the 'buzz-pollination' plants. This remarkable group of plants has anthers that only release their pollen when a pollinator 'buzzes' at the right frequency close to them. Local examples include species such as lady's hand (*Cyanella* species) and bitter apples (*Solanum* species). As in the case of our orchids and carrion flowers I have not yet seen any of these buzz-pollinated plants close their flowers at night.

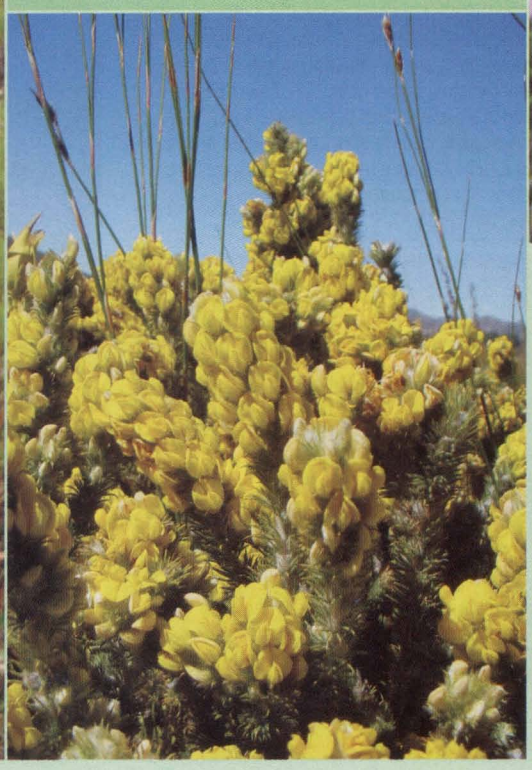
Erica species are not buzz-pollinated plants but they often only release their pollen through small apical pores and as far as I know none of them close their flowers at night or during wet weather. So there are all sorts of anther designs that plants have discovered to overcome the wet pollen problem, but there is more to the story. I believe some plants also have specific flower designs to overcome this problem.

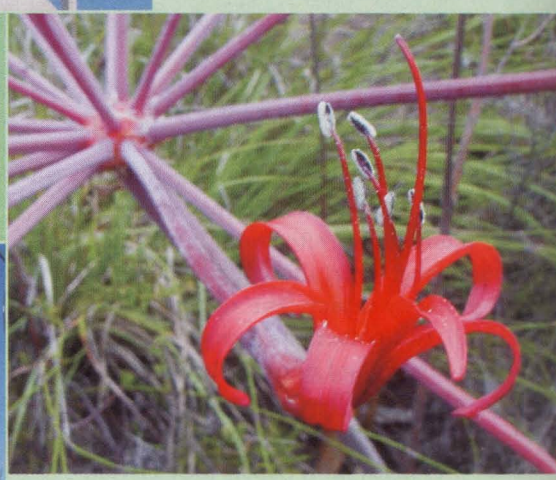
An interesting example of special flower design occurs amongst the vygies (ice plants). Flowers of the genera *Erepsia* and *Smicrostigma* are unusual amongst the vygies as they do not close their flowers at night. Why not? They are the only vygies that hide their anthers underneath a tightly closed cone of staminodes (filaments without anthers) that is watertight. To pollinate these vygie flowers, beetles actually have to

LEFT: What's the buzz? *Cyanella orchidiformis* is one of the remarkable 'buzz-pollinated' plants that only releases its pollen through a narrow pore when an insect buzzes at the correct frequency close by. The pollen is naturally protected against moisture and the flowers remain open in cool conditions.

FAR LEFT: *Erepsia pentagona* is an unusual vygie that remains open at night and even during rain. The tight cone of staminodes (filaments without anthers) in the centre of the flower covers the anthers and ensures that no moisture can reach the pollen. Photos: Jan Vlok.

Some plants may even dictate to their pollinators how they should behave





ABOVE: *Brunsvigia josephiniae* is one of many plants that only flowers in the dry season, usually in arid areas. Their flowers remain open in the evening, but as it is usually dry, there is little risk of their pollen getting wet. Photo: Jan Vlok.

FAR LEFT:
If you ever wondered why orchid flowers do not close at night, I would say that it is because their pollen is well protected in little waterproof bags. Those flowering during the rainy season, like the ewwa-trewwa *Satyrium coriifolium*, seem to have taken extra protective measures by having an 'anther-umbrella' flower design as well.

LEFT: An interesting variation on the normal theme of flower display occurs amongst legumes such as *Aspalathus shawii*. None of these close at night or during rain, simply because their pollen is well protected in the boat-shaped keel at the base of the flower. Photo: Jan Vlok.

ABOVE: A variation on the 'windsock' design is the 'anther-umbrella' design. The flower stem is sturdier and the flowers open wider for maximum advertisement to pollinators, but an 'umbrella' ensures that the anthers cannot easily get wet during rain. A typical example is the kalkoentjie *Gladiolus equitans* that often prefers to grow in somewhat dry areas. Photo: Jan Vlok.

break their way through the cone of staminodes.

Then there is another interesting option in flower design to protect pollen from getting wet that I call the 'windsock design'. Fine examples of 'windsock-flowers' are the bluebells (*Gladiolus* species) of the winter rainfall area and the harebells (*Dierama* species) of the summer rainfall area. None of these 'windsock' flowers close at night or during inclement weather, but they do not have to. The tubular-bell shaped flowers sit on thin flexible stems that swing the open end of the flower away from any moisture-laden wind in the slightest breeze. This flower design may be doubly clever, because I suspect that certain insects use these 'windsock' flowers as safe homes to escape inclement weather conditions. While they hide in the flowers during cool, wet conditions, they pick up the pollen and take it to the next flower as soon as the weather improves.

Another option that some plants seem to use to ensure that their pollen does not get wet is simply to flower during the dry season. But in order to do this, plants must have access to stored resources. Species that do not produce waterproof anthers or fancy flower designs, but are able to produce bulbs or corms in which resources can be stored, have gone for this option. Perhaps the best examples I know of are members of the amaryllis family in the Western Cape. Most amaryllid flowers, kukamakrankas, red nerines and candelabra flowers, flower during the driest time of the year.

Ever since Richard's initial question, I have found many new ways to look at plants. His simple question has added a lot of pleasure to the joy of looking at flowers in the veld and in my own garden. For me, flowers are no longer just pretty faces. I can see all sorts of ingenious shapes, designs and behaviour in them. A delightful new insight is the possibility that flower shape and behaviour may not be driven by what scientists would call 'pollination-syndromes' which implies that insects and animals will dictate to flowers how they should look and behave, but that some plants may even dictate to their pollinators how they should behave.

WHAT DOES THAT MEAN?

anther upper potion of the stamen that produces the pollen
filament: the stalk of an anther, usually thread-like
ovary part of the female organ consisting of one or more chambers containing the ovules
pistil the female part of the flower comprising the stigma, style and ovary
stamen the male part of the flower, comprising an anther and its filament
staminodes filaments without anthers
stigma tip of the style or style branches that picks up the pollen grains during pollination
style the thread-like stalk connecting the ovary to the stigma

BotSoc link

Jan Vlok is a Life Member of the Botanical Society and a well-known botanical consultant resident in Oudtshoorn. He has recently been appointed to the position of Project Co-ordinator of the Gouritz Initiative, a project under the banner of Cape Action for People and the Environment (C.A.P.E.)