TOWARDS AN UNDERSTANDING OF WIND DISPERSAL OF *ACACIA* POLLEN IN SOUTHEAST TASMANIA

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(with two figures, three tables and two appendices)

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Since 2015, daily atmospheric pollen samples have been collected on the University of Tasmania campus in Sandy Bay, Hobart, and classified according to botanical origin. We used this database to relate temporal variation in daily catch of *Acacia* pollen to both the flowering phenology of 16 species growing within 300 m of the sample point and to ambient weather conditions. Flowering was observed between July and December 2023. Only *A. baileyana* was flowering in early July and only *A. mearnsii* in December. Peak flowering of most other species co-occurred in August/September and pollen source could not be differentiated. Repeatability of the seasonal flowering pattern is demonstrated for 2016–2023. During the peak 2023 flowering season pollen catch was highest during periods of relatively warmer and windier weather, with wind speed at 3 pm on the day prior to the 9 am sample collection significantly associated with pollen count. Results are consistent with the proposition that, in addition to insects, wind may play a role as a pollen vector and that ambophily may be a more correct description of the pollination syndrome for these SE Australian *Acacias*.

Key Words: *Acacia*, flowering phenology, wind pollination, pollen dispersal, pollination syndrome, ambophily.

INTRODUCTION

Most species of *Acacia* exhibit an outcrossing breeding system, requiring transfer of pollen between different plants for successful seed set (Gibson *et al.* 2011). Published reviews of *Acacia* pollination ecology (Bernhardt 1989, Stone *et al.* 2003) focus strongly on the role of a diversity of insects as pollen vectors. However, over 80% of *Acacia* species native to SE Australia, flower in late winter to early spring (Costermans 2009), when there are relatively few insect visitors that are large and/or active enough to be efficient pollen vectors (Griffin *et al.* 2020). There is an increasing realisation that many plant species are best described as ambophilous, that is, exhibiting both biotic and abiotic pollen dispersal (Culley *et al.* 2002). This possibly includes some Australian Acacias (Giovannetti *et al.* 2018, Wandrag *et al.* 2023).

It is well established that some *Acacia* pollen can be dispersed by wind. For example, Smart and Knox (1979) reported airborne pollen in springtime Melbourne and the genus is also considered a potential allergen (Allergy & Autoimmune Disease 2022). In SE Tasmania, Tng *et al.* (2010) listed *Acacia* as the sixteenth most prevalent taxon in the pollen cloud sampled in Hobart over a calendar year, and cited comparable data from Sydney, Brisbane and Darwin. The unresolved issue is the extent to which such dispersion contributes to effective cross-pollination of different species of *Acacia*.

Since 2015, the AirRater program, conducted by the Menzies Institute in Hobart (Johnston *et al.* 2018) has collected daily records of airborne pollen from a rooftop on the University of Tasmania (UTas) Sandy Bay campus, to aid understanding of the medical impacts of variation in air quality. Twenty-seven distinct pollen taxa are classified to at least Family level, and, because of its distinctive polyad structure (Kendrick & Knox 1982), it is easy to observe and count pollen of genus *Acacia*.

In addition to its main health objective, the AirRater database also provides a unique opportunity for the study of diurnal and seasonal variation in dispersion of the pollen of each recorded plant taxon. The current study would have been impracticable without such access.

In 2023, we recorded the flowering phenology of 16 native and ornamental species of *Acacia* growing on the UTas Sandy Bay campus and, with reference to the AirRater database, related this to daily pollen catch. Using meteorological data from a nearby Bureau of Meteorology station, we also explored the relationship to weather conditions. For comparison with the pollen dispersion pattern of a specialised wind-pollinated species we also present data for *Pinus radiata* which flowers concurrently. Repeatability of the seasonal variation in the catch of *Acacia* pollen, and by inference species' phenology, was demonstrated through comparison of data for the eight years from 2016 to 2023.

METHODOLOGY

Local *Acacia* population

There are 21 native and seven naturalised species of *Acacia* in Tasmania (Jordan 2024). Additional species from the mainland are commonly planted as ornamentals. We recorded the flowering phenology of all individuals of the

16 species (six native to SE Tasmania and 10 introduced from elsewhere in the State or from mainland Australia), which are either planted or naturally occurring on campus within 300 m of the trap site (table 1). These species are taxonomically diverse, representing four different sections of the genus (Murphy & Maslin 2023). We are confident that all potential pollen donor species in the region were included in the survey.

Pinus radiata also flowers during August/September (Hetherington, S pers. comm.) and pollen catch data are presented for comparison with the *Acacia* results. There are no pine trees on campus, the nearest individual being 640 m to the NW; however, there are substantial commercial plantations in the region, the nearest being at Moogara 30 km to the NW of campus. Smaller plantings occur closer to Hobart on farms and parkland.

Flowering phenology

We observed all 228 *Acacia* plants within a 300 m radius of the trap location (appendix 1). This area represented a compromise between observational workload and need to demonstrate that the pollen was indeed capable of wind transport over significant distances. We divided the study area into 22 'locations' of varying sizes reflecting the patchy distribution of plants and recorded the number of individuals of each species at each location. Then, at approximately two-week intervals from the end of June 2023 (the first flowering of *A. baileyana*) to the conclusion of the flowering of *A. mearnsii* in December, we assessed the phenological state of groups of individuals within species within locations. From observations in earlier years, we knew that this period would cover the flowering of all species except *A. uncifolia*, a medium-sized shrub which was represented by five plants within an average of 60 m of the sample point (table 1).

All species except *A.uncifolia* have a single discrete flowering season of varying length, enabling phenology assessment by the scoring method described for trees in a nearby natural population of *A. dealbata* (Griffin *et al.* 2020). Where there was only one plant per species per location the percentage of open flowers was visually estimated on a decile scale from very few (<+10 %), to full flowering (100%) and then decreasing in negative deciles to -10%. With more than one plant of a species at a location the range of states from most to least advanced was noted and the modal value estimated. All records were collected by one observer. Although we scored all species, we only present analysis of the phenology data from the ten species with seven or more individual plants. These include the three natives of tree-form (*A. dealbata, A. melanoxylon* and *A. mearnsii)*. For the remaining species with small

TABLE 1 — *Acacia* species present on the University of Tasmania Sandy Bay campus and included in the 2023 phenology study

Species	Section (after Murphy & Maslin 2023)	Habit	Total no.	Mean distance (m) to pollen trap	Distance to nearest plant (m)	Status in region[1]
A. dealbata	Botrycephalae	tree	28	155	65	native
A. mearnsii	Botrycephalae	tree	60	170	35	native
A. baileyana	Botrycephalae	large shrub	15	255	185	introduced ex NSW
A. melanoxylon	Plurinerves	tree	15	80	35	native
A. boormanii	Acacia[2]	small shrub	24	115	65	introduced ex NSW/Vic
A. cultriformis	Acacia[2]	small shrub	2	100	100	introduced ex NSW/Qld
A. fimbriata	Acacia[2]	small shrub	2	210	185	introduced ex NSW/Qld
A. howittii	Acacia[2]	large shrub	30	210	35	introduced ex Vic
A. pravissima	Acacia[2]	large shrub	21	170	35	introduced ex NSW/Vic
A. pycnantha	Acacia[2]	small shrub	1	100	100	introduced ex SA/Vic
A. stricta	Acacia[2]	small shrub	2	240	240	native
A. uncifolia	Acacia[2]	large shrub	5	60	35	native to Tas but not SE region
A. floribunda	Juliflorae	small shrub	8	150	150	introduced ex NSW/Qld
A. longifolia	Juliflorae	large shrub	7	160	100	introduced ex NSW/Vic
A. mucronata	Juliflorae	small shrub	1	35	35	native
A. verticillata	Juliflorae	small shrub	7	100	100	native
			228			

[1] distribution information ex *Flora of Australia*

[2] syn. Sec. Phyllodineae

observable populations, we simply tabulate the first and last dates on which open flowers were observed on one or more plants (app. 2). Distance from each location to the pollen trap was recorded and used to calculate a weighted mean distance for the population of each species (table 1), as a basis for qualitative discussion of the probability of being a source for trapped pollen.

Pollen capture

Pollen data were collected by the AirRater pollen monitor located on the roof of the UTas Life Sciences building, Sandy Bay, Hobart, approximately 11 m above ground level (app. 1). The pollen monitor is a standard Burkard volumetric sampler (Burkard Manufacturing Co. Ltd, Hertfordshire), fitted with a 24-hour head. Pollen samples were collected in accordance with the Australian Pollen and Spore Monitoring Interim Standard and Protocols (Beggs *et al.* 2018). The monitor draws in air at a rate of 10 L/minute through a narrow (2 x 14 mm) inlet. Pollen and other particles in the air are impacted onto a slide coated with Syglard adhesive. The slide moves slowly through the 24-hour sampling period, and pollen is distributed across its surface. The slides are collected and replaced daily at 9 am. After sample collection, three transects of pollen are counted at 400x magnification. The resulting pollen counts are ordinarily converted to atmospheric concentrations (grains/m^3) using the formula provided in Beggs *et al.* 2018. With the standardised assessment protocol, a conversion factor of 0.6481722 is applied, so a catch of 10 polyads equates to 6.48 polyads/m^3 over the 24-hour sampling period. However, for this study where relativities of daily, cumulative weekly, and monthly catches were of primary interest we chose to analyse raw 24-hour count data.

The distinctive polyad structure makes it easy to identify *Acacia* to generic, but not species, level so we are only able to infer likely source taxa from the phenological data and location of plants in relation to the trap.

Historical pollen records

Daily pollen samples have been collected continuously since October 2015. To assess yearly repeatability of the seasonal pattern of *Acacia* pollen catch we calculated the monthly total number of polyads captured for each year from 2016 to 2023 and present these in bar chart form.

Meteorological data

For the peak flowering months of August and September we accessed daily weather records from the Bureau of Meteorology station at Edgerly Rd, Hobart (Bom.gov.au. 2023). This is located 1.8 km to the north of the campus at a comparable elevation. We analysed the following variables: maximum daily temperature; rainfall; RH% at 3 pm; maximum wind gust; and wind speed and direction at 3 pm. It is important to note that these are 24-hour records midnight to midnight, whereas the daily pollen records are from 9 am to 9 am. It was therefore considered most informative to focus on weather for the day prior to each pollen count.

ANALYSIS

Phenology records

For each observation date, data for each species were pooled over locations and the modal stage of flowering of the total population plotted over time to represent the seasonal progression in phenology. For ease of graphical representation, stages were pooled into six classes and plotted on the same x-axis as the pollen catch data. For weeks that were not monitored we assumed an intermediate state between the two nearest observations.

Pollen data

The pollen count database was used in two ways. For demonstration of the seasonal variation in pollen catch and its relationship to phenology, we summed the daily pollen catch for each week from July–December and graphically aligned these totals with the plots of the phenological state of each species. When exploring relationships to meteorological conditions, we used individual daily records.

Meteorological data

During the months of August and September there were 18 days when zero *Acacia* pollen was recorded (designated as Set 1), and 10 days with a catch of 5 or more polyads (average 8.1) (Set 2). We used double ended t-tests to determine whether there was a significant difference between Sets for each weather parameter, and in the respective catches of pine pollen which were included to indicate the extent to which the weather effect is generalisable to other plant taxa. We used a Chi-squared test to assess the significance of variation in wind direction between Sets, based on the respective counts of the days from the SSW-N sector compared to NNE-S.

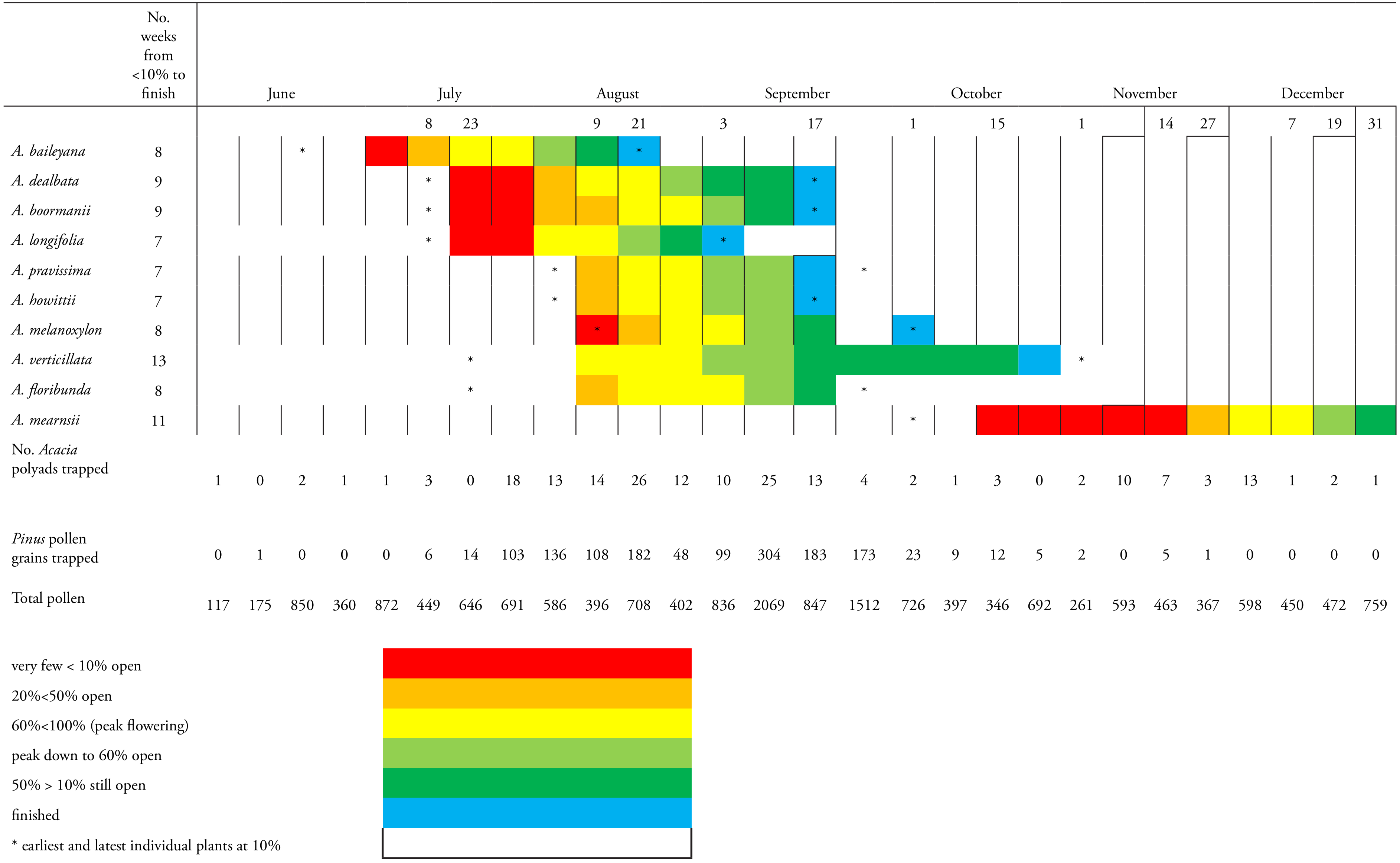
As a second approach, we identified the week with highest *Acacia* pollen catch in each of the months of July, August and September, and then compared prevailing weather conditions with the respective monthly mean values for each parameter.

RESULTS

Flowering phenology

Observation commenced at the beginning of July 2023 and continued to the end of December. The progression of flowering of each of the 10 species with a population size of seven or more (table 1) is shown in figure 1. Until the third week in July, only *A. baileyana* was in flower, finishing in mid-August. During mid-August to mid-September eight of the species flowered concurrently, with six at around peak flowering in the third week of August. These include

FIGURE 1 — Flowering phenology of 10 *Acacia* species with 7 or more individuals, aligned with weekly pollen catch. Observation dates are indicated. For weeks with no observations the most likely stages are interpolated. Catch of *Pinus* pollen over the same period is included for comparison.



	No. weeks from <10% to finish	June				July				August				September				October				November				December			
							8	23			9	21		3		17		1		15		1		14	27		7	19	31
A. baileyana	8			*		🟥	🟧	🟨	🟨	🟩	🟢	🟦 *																	
A. dealbata	9						*	🟥	🟥	🟧	🟨	🟨	🟩	🟢	🟢	🟦 *													
A. boormanii	9						*	🟥	🟥	🟧	🟧	🟨	🟨	🟩	🟢	🟦 *													
A. longifolia	7						*	🟥	🟥	🟨	🟨	🟩	🟢	🟦 *															
A. pravissima	7									*	🟧	🟨	🟨	🟩	🟩	🟦	*												
A. howittii	7									*	🟧	🟨	🟨	🟩	🟩	🟦 *													
A. melanoxylon	8										🟥 *	🟧	🟨	🟨	🟩	🟢		🟦 *											
A. verticillata	13							*			🟨	🟨	🟨	🟩	🟩	🟢	🟢	🟢	🟢	🟢	🟦	*							
A. floribunda	8							*			🟧	🟨	🟨	🟨	🟩	🟢	*												
A. mearnsii	11																	*		🟥	🟥	🟥	🟥	🟥	🟧	🟨	🟨	🟩	🟢
No. *Acacia* polyads trapped		1	0	2	1	1	3	0	18	13	14	26	12	10	25	13	4	2	1	3	0	2	10	7	3	13	1	2	1
Pinus pollen grains trapped		0	1	0	0	0	6	14	103	136	108	182	48	99	304	183	173	23	9	12	5	2	0	5	1	0	0	0	0
Total pollen		117	175	850	360	872	449	646	691	586	396	708	402	836	2069	847	1512	726	397	346	692	261	593	463	367	598	450	472	759

very few < 10% open	🟥
20%<50% open	🟧
60%<100% (peak flowering)	🟨
peak down to 60% open	🟩
50% > 10% still open	🟢
finished	🟦
* earliest and latest individual plants at 10%	☐

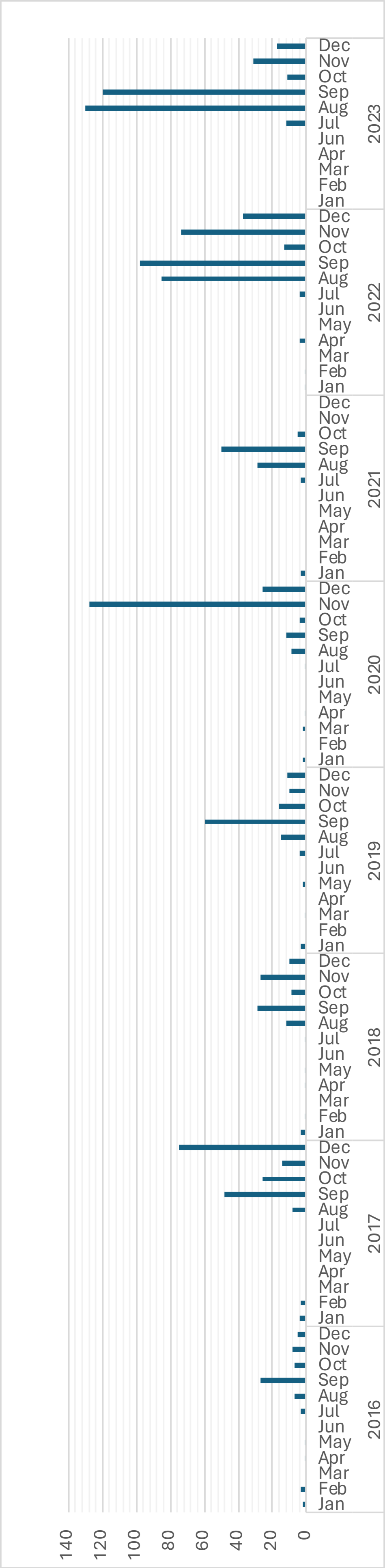


FIGURE 2 — Monthly total catch of *Acacia* pollen at the University of Tasmania Sandy Bay campus, over the years 2016–2023

representatives of all four taxonomic sections of the genus in the study (table 1). From late September through October, only two species (*A. melanoxylon* and *A. verticillata)* were in the later stages of flowering, with a few flowers opening on *A.mearnsii* from mid-October. Flowering of the latter species peaked in early December and was complete by the end of that month. The total flowering period of individual species ranged from seven (*A. longifolia*, *A. pravissima* and *A. howittii*) to 13 weeks (*A. verticillata*). In each species there were individual plants which produced a few flowers earlier or later than indicated by these ranges.

Repeatability of flowering patterns as inferred from the pollen records 2016–2023

The bimodal pattern observed in 2023 was also broadly evident in earlier years (fig. 2). Where this was less evident (in 2016, 2019, 2021) there was little or no pollen in November–December, presumably because of poor flowering in *A. mearnsii.* This is the only common species flowering in the region at that time and the most prevalent on campus with 60 trees including several within 35 m of the trap (table 1). Except in 2017 and 2022, when there was a particularly high November/December catch, most pollen was trapped in August–September, with temporal repeatability indicated by August being higher than July in all eight years, and September likewise always higher than October. Every year apart from 2021 there was also a small amount of pollen trapped during the period February–April. This is most likely from *A. uncifolia* which was the only species still in flower in March 2024 (Griffin unpubl. data) and capable of flowering throughout the year (Lynch 1994). In seven of the eight years, zero *Acacia* pollen was recorded in June, the exception being 2023 when, based on the phenology observations (fig. 1), the most likely source was *A. baileyana.*

Pollen catch profile for 2023

The pattern was distinctly bimodal with a major peak in August/September and a smaller one in November (fig. 1). From the phenological data in figure 1, only *A. mearnsii* was flowering at the latter time. From the end of July to the third week in September double-digit *Acacia* catches were recorded each week.

For quantitative comparison we also report the weekly catch of *Pinaceae* (almost certainly *P. radiata*) pollen and also the total of all 27 plant taxa combined. The pattern for *Pinus* mirrored that of most *Acacia* species, being highest from late July to the end of September; however, there was an order of magnitude difference in the amount of pollen caught in those nine weeks (135 polyads for *Acacia* and 1,336 grains for pine). The highest concentration of *Acacia* pollen on 22 September was 7.1 polyads/m^3, with the highest *Pinus* catch being 88.8 grains/m^3 on 14 September. For all plant taxa combined, the catch was 8,047. *Acacia* therefore represented only 1.7% of all pollen in the atmosphere.

TABLE 2 — Selected weather parameters for the day prior to days of zero (Set 1) or high (Set 2) pollen catches, during the months of August and September 2023

Observation dates	No. pine pollen grains	Max temp (°C)	RH% 3 pm	Max wind gust km/hr	Wind speed 3 pm km/hr	Wind direction 3 pm[1]
SET 1						
7-Aug	1	15.0	59	37	9	SE
9-Aug	5	15.3	57	28	17	ESE
15-Aug	9	12.0	51	26	11	ESE
16-Aug	10	13.1	50	26	9	NE
21-Aug	7	17.2	47	48	19	NW
23-Aug	5	12.4	87	46	7	SE
27-Aug	0	12.1	51	31	15	ESE
29-Aug	5	15.3	59	30	9	SE
30-Aug	0	19.3	41	44	17	NNW
3-Sep	3	13.7	59	28	15	SE
4-Sep	9	18.1	43	33	13	NNE
5-Sep	0	21.6	38	61	20	N
9-Sep	12	16.4	43	57	24	NNW
11-Sep	27	16.5	78	52	7	NNE
12-Sep	39	12.5	50	44	9	SE
18-Sep	44	17.3	35	87	35	WNW
20-Sep	0	22.9	21	104	21	NW
21-Sep	0	13.5	75	72	19	NW
SET 2						
10-Aug	50	14.1	47	44	13	N
19-Aug	37	13.3	52	56	20	SW
20-Aug	38	17.4	51	69	26	NW
22-Aug	44	19.1	38	65	35	WNW
25-Aug	57	19.0	44	50	26	NW
31-Aug	24	14.7	54	50	17	SSW
7-Sep	33	18.0	40	63	31	NW
15-Sep	46	20.9	64	41	15	E
16-Sep	43	20.3	36	72	30	NNW
22-Sep	1	11.9	73	50	28	SSW

	Set 1 - zero pollen	Set 2 - high pollen	Significance of difference (2-tailed t test)
Max temperature °C	15.8	16.9	n.s.
RH% 3pm	52.4	49.9	n.s.
Max wind gust (km/hr)	47.1	56.0	n.s.
Wind speed 3 pm (km/hr)	15.3	24.1	P<0.01
Rainfall (mm)	1.2	0.9	n.s.
Pine pollen catch	10	37	P<0.001

[1] By Chi-squared test, frequency of days with wind from SSW- N sector was significantly different between Sets (P<0.05).

Relationship between pollen catch and ambient weather conditions

The differences in weather variables for the Sets of days during August/September 2023 with zero and high *Acacia* pollen catches are shown in table 2. The only statistically significant relationship was with 3 pm wind speed, which was lower (15.3 km/hr) on zero days (Set 1) than the average of 24.1 km/hr on the days with high catch (Set 2). For six of the ten Set 2 days the 3 pm wind direction was between WNW and N. For the other traits, mean differences between Sets varied in the expected direction (relatively higher temperature, lower 3 pm RH% and higher maximum wind gust speed for Set 2) but there was sufficient variation within sets that these were not statistically significant. The average catch of *Pinus* pollen was also significantly less for Set 1 than for Set 2 (10 cf. 37 grains).

The weather records for each of the weeks of highest *Acacia* pollen catch in July, August and September respectively (fig. 1) showed that each includes a period of two or more days with higher temperature, lower RH% and more wind run than the respective monthly means (table 3). From the pattern of *Pinus* and total pollen catches during the high *Acacia* catch weeks it is clear that the weather conditions at those times was generally conducive to pollen dispersal. For *Pinus* the same weeks had the highest catch of the respective months (fig. 1) and for all three pollen categories the catch during those weeks was higher than for either the previous or following weeks.

DISCUSSION

The primary aim of the study was to increase understanding of the potential role of wind as a pollen vector for species of *Acacia* growing in SE Tasmania. This is important because the pollination syndrome of a species has a profound effect on its mating system and hence genetic structure of populations (Ellstrand 2014). Pollen flux will vary with the type of vector responsible for transfer between plants. Biotic vectors can have the advantage of effecting more precise pollination during feeding, but gene flow distances will be influenced by their behaviour, which may be quite localised. The populations of effective biotic vectors relative to the number of flowers requiring pollination, is also an important variable (Faegri & Van der Pijl 1979, Griffin *et al.* 2009). In contrast, wind can reliably disperse pollen over substantial distances (Robledo-Arnuncio 2011) and, for species with predominantly hermaphrodite flowers such as *Acacia*, the amount of pollen produced should vary directly with the number of ovules requiring pollination. The risk of pollen limitation should therefore be less than with biotic vectors. The seasonal phenology of a species determines probable weather conditions during flowering which will most likely impact the relative importance of insects and wind as pollen vectors.

Phenology and seasonal variation in pollen catch

Consistent with knowledge that a large proportion of *Acacia* species in SE Australia flower in late winter to mid-spring (Bernhardt 1989, Costermans 2009), all but three of the 16 species on campus completed flowering between late July and early October (fig. 1 and app. 2). The strong year-on-year repeatability of this pattern can be inferred from the pollen catch data (fig. 2). Tng *et al.* (2010) also reported that in 2007 local *Acacia* pollen catch was maximal in September. It is pertinent to note that species from four different taxonomic sections (table 1) were all flowering at this time suggesting that whatever evolutional force has shaped this aspect of the reproductive biology, it is general to the genus.

Pollen caught during early July can be attributed to *A. baileyana* (fig. 1), the nearest plant of which was 185 m from the sampler. The most common taxon in the study area, *A. mearnsii,* must be responsible for the secondary peak in pollen catch during November–December since it is the only species with significant flowering at that time. Moncur *et al.* (1991) reported that, following periods of medium to strong winds, they were able to trap pollen downwind of trees of this species. Variation in yearly amplitude of the November/December peak (fig. 2) is most likely due to variation in flowering intensity of the only flowering species, *A. mearnsii*. Its flowering in 2023 was relatively light while in 2021 a hot dry spring caused inflorescence buds to dry off prior to anthesis (Griffin

TABLE 3 — Meteorological conditions during weeks of highest *Acacia* pollen catch in 2023 for months of July, August and September (refer fig. 1 and table 2)

Month	Week	Total *Acacia* polyads	Two-day or more spell warm weather	Mean max temp °C	Mean 3 pm RH%	Total rainfall (mm)	Max wind gust (km)	Corresponding monthly mean values		
								Max temp	3 pm RH%	Wind gust
July	4	18	28–29/7	17.9	41.5	0.2	65	15.0	54.0	59
August	3	26	19–21/8	17.9	44.0	0.0	61	15.2	53.5	46
September	2	25	13–15/9	21.5	42.0	0.6	57	17.0	51.0	57

unpubl. observation). If reproductive output of *Acacia* is strongly limited by dependence on insect vectors, an adaptive shift to summer flowering might be expected, but except for *A. mearnsii,* this is not evident.

Pollen dispersion

The seasonal variation in pollen catch broadly reflected the flowering phenology (fig. 1) although we should not assume that all of the pollen did in fact originate on-site. The mean distance of plants from the pollen trap for the six species in full flower in late August, was 150 m (table 1). Of these only *A. dealbata* is of tree-form, with the nearest individual 65 m from the trap. There were several plants of the large shrubs *A. pravissima* and *A. howittii* 35 m from the trap building.

For the specialised wind-pollinated *Pinus*, a regional origin is clear since there were no trees on-site or even nearby. The most likely source was *P. radiata* which is extensively planted for wood production in Tasmania and flowers at the same time as the peak *Acacia* season (S. Hetherington pers. comm.). Griffin (1980) found that pollen density of this species attenuated over about 200 m from a point source on a calm day but was uniform for at least 1 km on a day with wind run averaging over 21 km/hr, so transportation over tens of kilometres would not be unusual.

Relationship with weather conditions

The particular weather variables analysed were chosen with reference to the literature. In general, pollen dispersion is favoured by dry warm conditions (Niklas 1985, Shramm *et al.* 2021). Stone *et al.* (1998) found that anthesis in species of Africa *Acacia* spp. was strongly correlated with ambient Relative Humidity (RH)%. Air turbulence is an important determinant of airborne pollen dispersion (Knox 1979) and Prescott (2005) reported that pollen shed from a number of *Acacia* species in Victoria was greatest from late morning to mid-afternoon. Niklas (1985) also refers to the phenomenon of ‘raindrop scavenging’ or the elimination of airborne pollen by rain.

Atmospheric conditions affect two distinct aspects of the reproductive processes – anther dehiscence and hence the availability of pollen for dispersion, and the transport of pollen *per se* (Niklas 1985). Irrespective of wind speed, pollen will not be captured if preceding conditions, particularly RH% (Stone *et al.* 1998), are not conducive to dehiscence. Conversely, pollen will not be dispersed from dehisced anthers unless wind speed passes some critical threshold. A wind tunnel experiment (Griffin unpubl. data) has shown that *A. dealbata* pollen begins to blow off flowers once the wind speed reaches 10 km/hr, with quantities increasing linearly to at least 35 km/hr. In this study we were not able judge the extent to which these traits separately affected pollen catch; however, from the significant association with 3 pm wind speed it is reasonable to assume that on days with relatively high catch, the temperature and RH% were adequate for dehiscence and therefore we had observed the effect of wind speed on dispersal. Mean wind speed on those days was 24.1 km/hr compared to 15.3 km/hr on days with zero catch (table 2). However, since wind speed was less than 10 km/hr on only six of the 18 zero catch days, it seems likely that weather effects on dehiscence were also important.

Pollen flux

Aside from the ambient weather conditions, seasonal phenology and density of the plant population, pollen flux will be influenced by the amount of pollen produced per plant which will vary with the number of flowers and the pollen grains per flower. Acacia flowers typically bear many stamens. Flowers of one of the dominant local species, *A. dealbata,* contain an average of 33 stamens (Correia *et al.* 2014). Each stamen carries a two-locule anther commonly containing 8 x 16 grain polyads which is a distinctive feature of this and other genera of Mimosaceae. Cruden (1977) reported a wide variation in the pollen:ovule (P/O) ratio of flowering plant taxa with different breeding systems, averaging over 5,000 for obligate outcrossers and less than 200 for those which are self-fertile. Bernhardt (1984) estimated a P/O ratio of 640 for *A. retinodes* which, if we accept that *Acacias* are generally outcrossers, is on the low side. However, it is common to find that some flowers within a head are only male, and if we consider the multi-flowered inflorescence to be the effective pollination unit (Kendrick 2003), the ratio will be correspondingly increased. A distinctive feature of *Acacia* is that pollen grains are also clustered in polyads (Coetzee 1955, Kendrick & Knox 1982) with the number of grains comparable to the number of ovules per flower, so a single polyad alighting on a stigma is sufficient for full seed set. Cruden (1977) described this as a ‘sweepstakes’ pollination system, i.e., there is a low probability of successful pollen transfer, but a high reward in terms of seed set when this does occur. An *Acacia* polyad is relatively large (39 <70μ) (Coetzee 1955) and similar in size to *Pinus* pollen grains (45<65μ) (Cain 1940), each of which has two air sacs assisting flight. Loss of water content on release influences both the mass and form of pollen (Niklas 1985). Niklas observed that ‘the corpus of *Pinus taeda* grains assumes a concave-convex shape effecting a botanical "frisbee"’ (Niklas 1985, p. 335). Although unproven, the furrowed disk-like form of a polyad (Coetzee 1955) may have similar aerodynamic benefits.

The amount of flowers and therefore pollen produced will vary between *Acacia* species of different plant forms, but is clearly nowhere near that of *Pinus*. Khanduri and Sharma (2002) estimated a P/O ratio of about 5,000 for *P. roxburghii* and a mature radiata pine tree can produce up to 0.75 kg of pollen or 300 kg/ha of plantation every year (Scion 2017). It is therefore not surprising that our catch of pine pollen was an order of magnitude higher than for *Acacia* (fig. 1).

Different pollens have a characteristic settling velocity under calm conditions (Gregory 1973) with concentration downwind of a point source diminishing at a rate inversely proportional to the square of the distance travelled (Niklas 1985), but this no longer holds as turbulence increases (Faegri & van der Pijl 1979, Knox 1979, Sedgley &

Griffin 1989). In general, turbulence is much stronger than the rate of fall of pollen grains (Gregory 1973) and the gradual attenuation of pollen content in the air is due to diffusion rather than fall out (Faegri & van der Pijl 1979). Pollen dispersion is therefore most likely different from *Acacia* species with different growth habit, being greater from trees than smaller shrubs. Knox (1979) illustrated the point with a calculation that pollen released from a height of 1 m might travel 67 m before deposition whereas with release at 20 m it would travel 1,333 m. Each of the regionally common tree-form species, *A. dealbata* and *A. melanoxylon* (which flower during August–September), and *A. mearnsii* (November–December*),* can grow substantially taller than this and it seems highly likely that some of the *Acacia* pollen originated beyond the study area. In the context of pollination within natural populations, wind dispersal beyond 300 m could effect crosses between many different genotypes, not only within but between populations, and could explain the mechanism of gene flow between disjunct populations up to 1.9 km apart in *A. woodmaniorum* reported by Millar *et al.* (2014). Those authors suggested wind dispersion, but of pollen-bearing insects, rather than of polyads *per se.*

It is clear from the week-to-week variation in catch (fig. 1) that pollen is not shed uniformly through the flowering season of any of the species; however, given the rather lengthy flowering period of the spring-flowering species (an average of nine weeks) it is extremely likely that they will experience periods of suitable weather conditions at some point (see table 3). Weeks which were high for *Acacia* pollen also had particularly high catches of *Pinus* and total pollen (fig. 1, table 3) so it is reasonable to conclude that such conditions are generally favourable for pollen dispersion.

The fact that *Acacia* pollen can be wind-dispersed is not new. However, the idea that the pollination syndrome of this large, Australia-wide genus, should more correctly be described as ambophily is not well-developed in the literature. For two of the early flowering species in this study, there is supportive evidence. In Portugal, Giovanetti *et al*. (2018) reported pod set on *A. longifolia* within insect exclusion bags and argued for a role of wind as a vector. Secondly, the locally common species *A. dealbata* is known to set heavy crops of seed in the absence of substantial populations of biotic vectors (Griffin *et al*. 2020). Genetic analysis by Broadhurst *et al.* (2008) confirmed that NSW populations of this species are strongly outcrossed, which leaves wind as a likely vector responsible for the high level of cross-pollination inferred from the local seed crops. The phenology data reported in the current study confirmed the high concentration of flowering of temperate *Acacias* in late winter–early spring. If reproductive output is strongly limited by dependence on insect vectors one might expect an adaptive shift towards summer flowering, which, apart from *A.mearnsii,* is not apparent. We have been able to show that during July–September there were periods of weather conducive to pollen dispersion although at much lower levels than that observed for the specialised wind-pollinated *Pinus radiata*. Whether the observed flux is sufficient to effect a high level of seed set will require species- and population-specific field investigations.

The importance or otherwise of wind pollination has major implications for understanding the reproductive system, gene flow and population structure of *Acacia* species and justifies ongoing experimental studies designed to demonstrate the efficacy of wind, an ever-present feature of the weather in SE Tasmania, as a pollen vector. This is a challenging task requiring careful selection of a model species and study site; timely insect exclusion bagging; parallel quantification of insect visits; full environmental monitoring; and adequate replication to demonstrate statistical significance.

In a wide-ranging review of key questions in pollination ecology research, Mayer *et al.* (2011) noted increased reports of anemophily in otherwise entomophilous plant families (see also Culley *et al.* 2002). They identified key research questions: when, where and how did evolutionary shifts from biotic to abiotic pollination systems occur?; what are the biophysical mechanisms involved in abiotic pollination?; and is ambophily a stable or transitory evolutionary phenomenon? There are currently 1,082 described species in the genus *Acacia* (Murphy & Maslin 2023), adapted to a wide range of environmental conditions from Papua New Guinea through arid zone Australia to the temperate SE regions. About one-third of these are small- to medium-sized trees, a plant form favouring wind dispersion of pollen under suitable weather conditions, and the genus would be well-suited for comparative study of these unresolved questions.

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APPENDIX 1

The University of Tasmania's Sandy Bay campus showing study area within 300 m of pollen sampler on Zoology building roof. Scale bar represents 100 m.

APPENDIX 2

Flowering phenology of minor species observed in the 2023 phenology study on University of Tasmania Sandy Bay campus

Acacia species	Section[1]	Habit	Total no plants	Mean distance (m) to pollen trap	Distance to nearest plant (m)	Date of first flowering	Date of last flowering[2]
A. cultriformis	Acacia[3]	small shrub	2	100	100	Aug. 15	Sep. 17
A. fimbriata	Acaci [3]	small shrub	2	210	185	July 29	Sep. 17
A. pycnantha	Acacia[3]	small shrub	1	100	100	Sep. 7	Nov. 14
A. stricta	Acaci [3]	small shrub	2	240	240	Aug. 28	Oct. 1
A. uncifolia[2]	Acacia[3]	large shrub	5	60	35	July 8	(March 2024)
A. mucronata	Juliflorae	small shrub	1	35	35	Aug. 21	Oct. 1

[1] After Murphy & Maslin 2023.
[2] Species still flowering beyond end of this study until at least March 2024 and presumed responsible for five polyads recorded in January and two in February 2024.
[3] syn. Section Phyllodineae.