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## The persistence of ripe fleshy fruits in the presence and absence of frugivores

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**Abstract** A trade-off between antimicrobial defences and palatability to dispersers may place limits on fruit persistence in nature. The retention times of ripe fruits on 34 wild plant species under natural conditions (unbagged persistence) and when fruits had been bagged with nylon mesh to exclude frugivores (bagged persistence) were compared in Hong Kong, China (22°N). Bagged persistence is a measure of the effectiveness of fruit defence while unbagged persistence is an inverse measure of attractiveness to vertebrate frugivores. Bagged fruits persisted significantly longer than unbagged fruits in 30 species, with half the species tested persisting for more than 2 months. There was a significant positive relationship between the median persistence times of bagged and unbagged fruits, suggesting that species with a high resistance to microbial infection are also less attractive to frugivores. Both bagged and unbagged fruits persisted significantly longer at lower temperatures. There was a significant positive relationship between bagged persistence time and fibre content of the fruit pulp, but no significant relationships between unbagged persistence and the six fruit traits tested (diameter, pulp as a percentage of fruit fresh weight, and lipid, total soluble carbohydrate, nitrogen and fibre as percentages of pulp dry weight). Mechanical damage significantly decreased the bagged persistence time for half of the species. Although some fruits decayed or dried up while attached to the plant, fruits of 53% of the species remained visually attractive until they fell off.

**Keywords** Chemical defences · Frugivory · Seed dispersal · Microbes · Mechanical damage

### Introduction

It is obvious to every field biologist that there is a great deal of variation between species in terms of how long fleshy fruits persist on the plant after ripening. In one of the few systematic studies of this phenomenon, the mean persistence times of common fruit species in eastern North America varied from 3 to > 165 days (McCarty et al. 2002). Simple observations, however, cannot distinguish between fruits that are removed by vertebrates and those that are lost to microbial decay or inherent processes of senescence. These distinctions are important because of the very different consequences for the plant, the frugivores and the microbes. Rewards for vertebrate dispersal agents are equally attractive to microbes, and many antimicrobial compounds are likely to be equally unattractive to vertebrates, so a trade-off between attracting dispersal agents and avoiding microbial decay may place limits on fruit persistence (Cipollini and Stiles 1993; Cipollini and Levey 1997). The ability to retain ripe fruits in an attractive condition for a prolonged period will be particularly advantageous for plant species that depend on rare or unreliable seed-dispersal agents. This ability may also become crucial for survival in degraded tropical landscapes, because such landscapes lose dispersal agents much more rapidly than they lose plant species (Corlett 2002). Piles of rotting fruit under the parent tree are one of the characteristic signs of a botanically intact but zoologically impoverished tropical forest.

The major aim of the study reported here was to compare how long ripe fleshy fruits persisted on tropical plants exposed to frugivores with how long they persisted when frugivores were excluded with nylon bags. Persistence in the presence of frugivores will depend on both fruit attractiveness and frugivore availability. Persistence when frugivores are excluded is an indirect measure of fruit defence against microbes and those invertebrates that are small enough to enter the bags. An attempt was also made to distinguish between fruits that

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retained their visual attractiveness until they fell off and those that did not. Finally, the impact of mechanical damage, such as that caused by insects, on fruit persistence times was investigated. This study compliments a study of the diversity of fungi growing on wild fruits in the same area (Tang et al. 2003).

### The study area

Hong Kong (22°17'N, 114°09'E) has a subtropical monsoon climate, with hot wet summers and cool dry winters (Dudgeon and Corlett 1994). The mean monthly temperature ranges from 15.8°C in January to 28.8°C in July. The natural vegetation must have been evergreen or semi-evergreen forest, but centuries of human impacts have left a degraded landscape with a rich flora and an impoverished vertebrate fauna (Corlett 2002). Woody vegetation is dominated by a well-dispersed subset of the flora, while most plant species are rare. An estimated 27% of the ca. 2,000 native angiosperm species bear

fleshy, presumably vertebrate-dispersed, fruits (Corlett 1996). Although some ripe fruits are available throughout the year, there is an annual maximum in ripe-fruit abundance and diversity in December and January (Corlett 1993). Plant names follow Wu et al. (2001).

### Materials and methods

Thirty-four plant species in 21 families, with a variety of growth forms, were included in the study (Table 1). For each species, 3 sets of 20 newly ripe fruits were tagged with cotton sewing threads. One set was left exposed to frugivores while the others were bagged with nylon netting to exclude vertebrates. In one of the two bagged sets, a 3-mm-long cut through the skin was made with a sterilized scissors blade. The tagged fruits for each species were spread over four to eight individual plants, depending on ripe fruit availability, with no more than five fruits for each treatment on each plant, and with the plants used for the same treatments at least 10 m apart.

**Table 1** Persistence times of 34 ripe-fruit species in Hong Kong. Mann–Whitney tests were used to compare median persistence times of unbagged and bagged fruits (*U-B*) and undamaged and damaged bagged fruits (*B-D*). Final fates of bagged fruits were classified as remaining visually attractive until falling (*A*) or

becoming unattractive before falling (*U*) (*T* mean temperature during the persistence period, *U*, *B* and *D* median persistence times of unbagged, bagged and damaged bagged fruits, respectively; \**P* < 0.05, \*\**P* < 0.01, \*\*\**P* < 0.001, *NS* not significant)

Family	Species	Abbreviations	Fruiting	Habitat	Temperature (°C)	Persistence (days)			Mann-Whitney		Fate
						U	B	D	U-B	B-D	
Apocynaceae	<i>Alyxia sinensis</i>	AS	Nov–Dec	Sun	20	7	142	69	***	***	A
Aquifoliaceae	<i>Ilex asprella</i>	IA	May–Jun	Sun	28	14	24	15	***	***	A
	<i>I. cinerea</i>	IC	Nov–Dec	Sun	20	37	67	22	***	***	A
	<i>I. pubescens</i>	IP	Dec–Jan	Sun	18	45	137	115	***	*	A
	<i>I. viridis</i>	IV	Dec–Jan	Sun	18	39	85	98	***	NS	A
Araceae	<i>Alocasia odora</i>	AO	May–Jun	Shade	28	6	6	6	NS	NS	A
Araliaceae	<i>Schefflera heptaphylla</i>	SO	Mar–Apr	Sun	23	20	29	29	***	NS	A
Arecaceae	<i>Phoenix hanceana</i>	PH	July–Aug	Sun	29	15	21	15	**	NS	A
Caprifoliaceae	<i>Viburnum odoratissimum</i>	VO	July–Aug	Sun	29	15	42	28	***	NS	U
	<i>V. sempervirens</i>	VS	Nov–Dec	Sun	20	40	48	35	***	***	U
Chloranthaceae	<i>Sarcandra glabra</i>	SG	Dec–Jan	Shade	18	63	79	79	***	NS	A
Daphniphyllac	<i>Daphniphyllum calycinum</i>	DC	December	Sun	18	7	90	40	***	***	U
Ebenaceae	<i>Diospyros vaccinioides</i>	DV	Nov–Dec	Sun	20	59	163	121	***	***	A
Hydrangeaceae	<i>Dichroa febrifuga</i>	DF	January	Shade	17	223	128	93	***	***	U
Lauraceae	<i>Litsea rotundifolia</i>	LR	Oct–Nov	Sun	24	21	87	66	***	NS	A
Maesaceae	<i>Maesa montana</i>	MM	Dec–Jan	Shade	18	45	134	108	***	NS	U
	<i>M. perlarius</i>	MP	Dec–Jan	Sun	18	22	92	63	***	NS	U
Myrsinaceae	<i>Ardisia crenata</i>	AC	Dec–Feb	Sun	18	43	99	161	*	*	U
	<i>A. punctata</i>	AP	Dec–Feb	Shade	18	54	98	98	***	NS	U
	<i>A. quinquegona</i>	AQ	Nov–Dec	Shade	20	34	127	70	***	***	A
	<i>Embelia laeta</i>	EL	May–Jun	Sun	28	15	15	15	NS	NS	A
Myrtaceae	<i>Cleistocalyx operculatus</i>	CO	Sep–Oct	Sun	27	5	8	5	***	**	A
Phyllanthaceae	<i>Antidesma venosum</i>	AV	Sep–Feb	Shade	22	43	53	53	**	NS	U
	<i>Bridelia tomentosa</i>	BT	Jan–Feb	Sun	18	26	62	54	***	NS	A
Pittosporaceae	<i>Pittosporum glabratum</i>	PG	March	Shade	22	24	44	24	***	**	A
Rhamnaceae	<i>Berchemia floribunda</i>	BF	Mar–Apr	Sun	23	20	20	20	NS	NS	A
Rosaceae	<i>Rhaphiolepis indica</i>	RI	Dec–Jan	Sun	18	17	70	70	***	NS	U
	<i>Rubus reflexus</i>	RR	May–Jun	Sun	28	7	14	14	***	NS	U
Rubiaceae	<i>Diplospora dubia</i>	DD	Nov–Dec	Sun	20	71	85	46	**	***	U
	<i>Gardenia jasminoides</i>	GJ	Dec–Jan	Sun	18	34	41	41	NS	NS	U
	<i>Psychotria asiatica</i>	PA	Nov–Jan	Shade	19	33	53	32	*	*	U
	<i>P. tutcheri</i>	PT	Nov–Jan	Shade	19	70	205	165	***	*	U
Thymelaeaceae	<i>Wikstroemia nutans</i>	WN	Apr–May	Shade	26	15	57	36	***	***	A
Zingiberaceae	<i>Alpinia chinensis</i>	AL	Sep–Feb	Shade	22	62	158	118	***	**	U

The fruits were counted every 7 days for the first 2 months and every 14 days thereafter, until all fruits were removed or had fallen. The persistence time was recorded for individual fruits. Fruit persistence time was defined as the number of days that a fruit remained on the plant after it became ripe. The final fate of the undamaged bagged fruits was recorded as either remaining visually attractive until they fell off or drying out or looking unattractive for other reasons before they fell off.

Most variables were not normally distributed so medians are used to describe central tendencies and non-parametric tests for most comparisons. Mann-Whitney tests were used to compare the median persistence times of bagged and unbagged fruits of each species, and of damaged and undamaged bagged fruits. The median persistence times for all species of bagged and unbagged fruits, and of damaged and undamaged bagged fruits, were compared using Wilcoxon signed rank tests. The relationships between bagged and unbagged persistence, and between these and the mean daily temperature during the persistence period, were investigated with linear regression. Mann-Whitney tests were used to compare the persistence times (both bagged and unbagged) of sun fruits (shrubland and forest canopy species) and shade fruits (forest understorey). The relationships between bagged and unbagged persistence and six fruit traits (diameter, pulp as a percentage of fruit fresh weight, and lipid, total soluble carbohydrate, nitrogen and fibre as percentages of pulp dry weight; from Corlett 1996) of individual species were tested using Spearman's rank correlation coefficient and linear regression. All the statistical analyses were done with SigmaStat. We have not controlled for possible phylogenetic effects, because of gaps and uncertainties in the phylogenetic information available for the species compared. This may have resulted in inflation of the degrees of freedom, although the range of persistence times among congeneric taxa (Table 1) suggests that the major relationships are not phylogenetic artefacts.

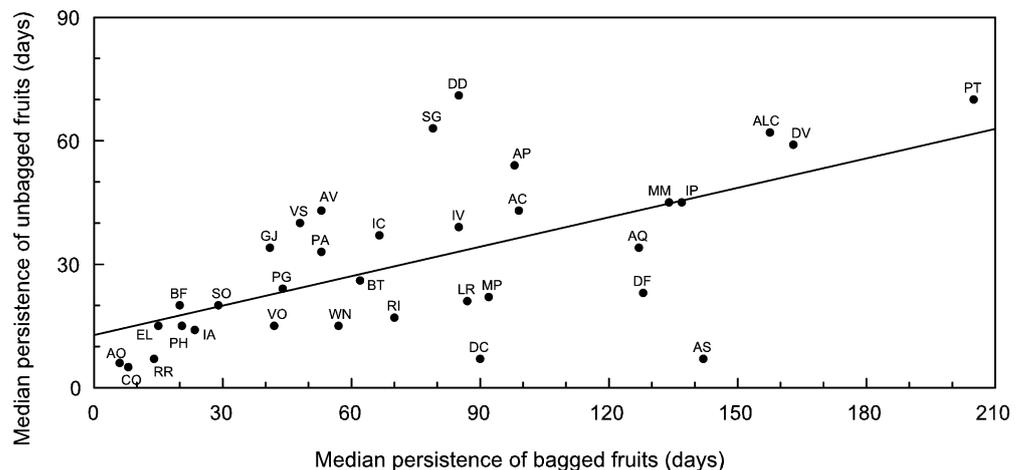
## Results

All fruits species persisted longer when protected by nylon netting and this difference was significant in all species except *Alocasia odora*, *Embelia laeta*, *Berchemia floribunda* and *Gardenia jasminoides* (Table 1, Fig. 1). The median persistence times of unbagged and bagged fruits across all species were significantly different ( $P < 0.001$ ; Wilcoxon signed rank test). Of the fruit species surveyed, 47% persisted  $< 2$  times as long when frugivores were excluded, 35% persisted 2–4 times as long, and 18%  $> 4$  times as long. The lowest ratios of bagged to unbagged fruit persistence were in *Alocasia odora*, *B. floribunda* and *E. laeta* and the highest ratio was in *Alyxia sinensis*. Approximately half (53%) of the fruit species remained visually attractive until they fell off while the remainder became unattractive while still attached to the plant.

In the presence of frugivores (unbagged), 53% of the species had their fruits completely removed within a month, 88% had their fruits totally removed within 2 months and no fruits persisted more than 3 months (Fig. 1). In the absence of frugivores (bagged), in contrast, 76% of fruit species persisted for more than a month, 56% for more than 2 months, 35% for more than 3 months, 24% for more than 4 months and 9% for more than 5 months. The median persistence of unbagged fruits varied from 5 days in *Alocasia odora* to 71 days in *Psychotria tutcheri*, while the median persistence of bagged fruits ranged from 6 days in *Alocasia odora* to 205 days in *P. tutcheri*. The relationship between median persistence times of bagged and unbagged fruits was positive and highly significant ( $R^2 = 0.383$ ,  $P < 0.001$ ) (Fig. 1). *Daphniphyllum calycinum* and *Alyxia sinensis* were outliers, with long persistence times when bagged but short persistence times when unbagged.

The relationships between both bagged and unbagged persistence times and the mean temperature during the persistence period were negative and highly significant ( $R^2 = 0.382$ ,  $P < 0.001$  and  $R^2 = 0.291$ ,  $P = 0.001$ , respec-

**Fig. 1** The relationship between the median persistence times of bagged and unbagged ripe fruits of 34 species (linear regression;  $R^2 = 0.383$ ,  $P < 0.001$ )



tively). Shade fruits persisted longer than sun fruits, bagged or unbagged, but these differences were not statistically significant (bagged  $P=0.101$ , unbagged  $P=0.069$ , Mann-Whitney test). Among the six fruit traits tested, only fibre content of the fruit pulp was significantly correlated with bagged persistence. The relationship between bagged persistence and fibre was positive ( $R^2=0.217$ ,  $P<0.05$ ,  $n=23$ ) (Fig. 2). However, summer fruits have significantly lower fibre than winter fruits in Hong Kong (Corlett 1996) and in a two-factor regression model with temperature, fibre did not explain a significant amount of additional variation. There were no significant relationships between any fruit trait and unbagged persistence ( $P>0.1$ ).

Mechanical damage significantly decreased the bagged persistence time for 50% of fruit species (Table 1), including 73% of long-persistent fruits ( $>3$  months median persistence time) and 36% of short-persistent fruits. The median persistence times of damaged and undamaged fruits across species were significantly different ( $P<0.001$ ; Wilcoxon signed rank test). Damaged fruits persisted significantly longer than undamaged fruits only on *Ardisia crenata*.

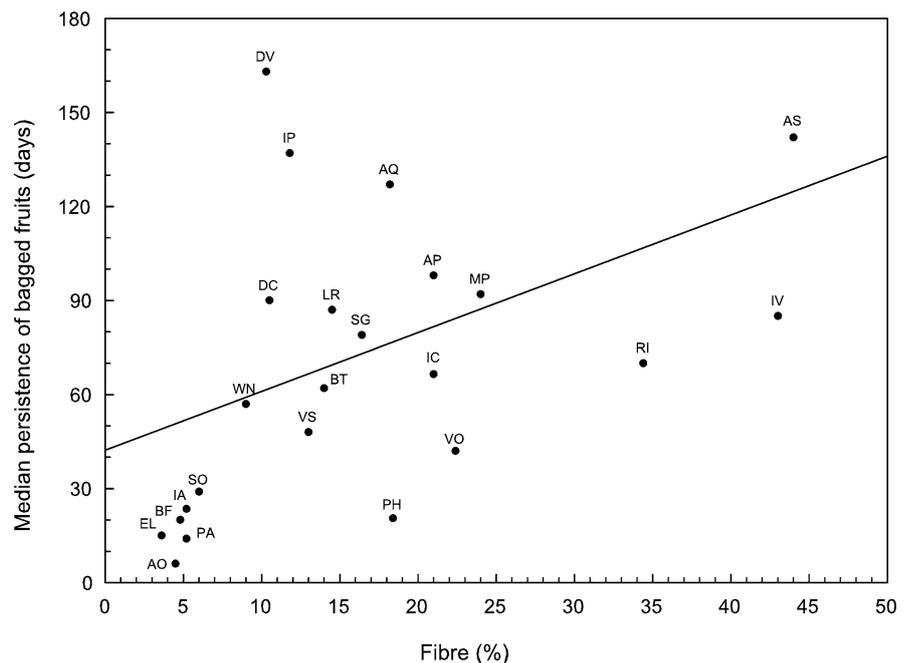
## Discussion

This is apparently the first multispecies study of fruit persistence times in the tropics. The median persistence times for unbagged ripe fruits in Hong Kong (5–71 days) are lower than some reported in the temperate zone, where many ripe fruits persist for several months ( $>6$  months in some cases) in winter (e.g. Stiles 1980; Kominami 1987; McCarty et al. 2002). The increased

persistence times when frugivores were excluded (6–205 days) suggest that these differences may largely reflect faster removal rates in Hong Kong, rather than a lesser ability to resist microbial decay. The only comparable data from the temperate zone are for six species of Ericaceae in which bagged fruits persisted 24–106 days before falling (Cipollini and Stiles 1992). The ability of more than half the plants species studied to retain ripe fruits for more than 2 months in the absence of frugivores implies that the plants can afford to wait for high-quality dispersal agents. If choosy plants meet choosy frugivores (Schaefer et al. 2003), there is an opportunity for the evolution of greater plant-disperser specificity, although there is currently rather little evidence that this has actually occurred (Herrera 2002; Brown and Hopkins 2002). Long fruit retention times also have implications for the design of field studies, since the fruit-removal rates required to disperse all the seeds ( $<2\%$  of ripe fruits per day for most plant species in this study) may be too low to measure by direct observations of fruiting plants.

The positive and significant relationship between bagged and unbagged persistence suggests that, in general, fruit species with a high resistance to microbial infection (i.e. those that persist a long time when bagged) are also less attractive to frugivores (i.e. they also persist a long time when accessible to frugivores). These results are consistent with the palatability-defence trade-off hypothesis of Cipollini and Stiles (1993), who showed that the highly fungal resistant fruits of *Vaccinium macrocarpon* are removed more slowly than the less resistant fruits of *V. corymbosum*. However, there are alternative explanations for this correlation, since any factor leading to low rates of removal by dispersers (e.g.

**Fig. 2** The relationship between the median persistence times of bagged fruits of 23 species and the fibre content of the fruit flesh (linear regression;  $R^2=0.217$ ,  $P<0.05$ ). Fruit species abbreviations follow Table 1



habitat, fruiting phenology, low nutritional reward) could lead to selection for longer persistence in the face of attack by microbes or invertebrates. Even if a palatability-defence trade-off is involved, the low  $R^2$  value (0.38) and the spread of points in the scatter plot show that other, independent, factors are also important in explaining attractiveness to frugivores.

Our results agree with many temperate-zone studies in which summer fruits persisted for a shorter time than winter fruits (e.g. Cipollini and Stiles 1992, 1993; McCarty et al. 2002). The longer persistence of unbagged fruits in winter is surprising in tropical Hong Kong, where both the density of avian frugivores and their dependence on fruits are highest in winter (Corlett 1998; unpublished work). However, fruit supply may exceed demand during this period, since there is a large winter maximum in fruit availability (Corlett 1993). Within the genus *Ilex*, the single summer-fruiting species, *I. asprella*, which is one of the very few plant species bearing ripe flesh fruits in June, had much lower bagged and unbagged persistence times than the three winter-fruiting species tested. The longer persistence time of bagged fruits in cooler months could reflect a higher inherent fungal resistance, but it is also likely that the risks of microbial decay and insect damage are lower during the cooler, drier winter months. Invertebrate diversity and abundance are much lower in winter (December-March) than in summer in Hong Kong (Kwok and Corlett 2002) and both lower temperature and lower humidity inhibit the growth of most microbes. The optimum temperature for microbial decay is within the range 18.5–26.5°C (Holliday 1980), which is higher than normal winter temperatures in Hong Kong, but lower than normal summer temperatures.

High-fibre fruits persisted longer when bagged. The scatterplot hints at a more complex relationship between these variables than shown by the linear regression, with low persistence times for low-fibre fruits and high persistence times for high-fibre fruits, but much more variability between these extremes (Fig. 2). The arrangement of the fibre in the fruits is not known, but it may form a mechanical defence. Gargiullo and Stiles (1991) showed that the more persistent fruits of *I. opaca* have a thicker sclereid layer around the epidermis than those of the less persistent *I. verticillata*. The rather surprising lack of correlation between unbagged persistence and any of the fruit traits tested suggests that other factors have more influence on attractiveness to frugivores. These factors are likely to include additional fruit traits, such as the presence of secondary metabolites, as well as the availability of frugivores, the time of fruiting, and competition with co-fruiting species for frugivores (Herrera 2002). Also, the fruit preferences of individual frugivore species may be obscured when removal by the whole frugivore community is assessed.

The significant effect of mechanical damage on most long-persistent fruits suggests that long persistence is associated, at least in part, with defences (physical or chemical) in the skin. Mechanical damage presumably

breaches the barrier formed by the outer skin, allowing entry of microbial spores. Exceptions were *Ardisia punctata*, *Maesa perlarius* and *M. montana*, where defences in the pulp may be more important. The significantly longer persistence time of damaged *Ardisia crenata* fruits suggests that defensive chemicals may have been induced by damage in this species. However, this was a crude, preliminary study and the responses of fruits to mechanical damage need further investigation.

Half (53%) of the fruit species remained visually attractive until they fell off. The reasons for shedding apparently attractive fruits are not known, but this behaviour is not necessarily maladaptive since several species of ground-feeding birds in Hong Kong, including resident laughingthrushes (*Garrulax* spp.) and winter-visitor thrushes (*Turdus* spp., *Zoothera* spp.), feed on fallen fruits. Conversely, almost half of the fruit species lost visual attractiveness while still on the plant. However, our subjective assessment of visual attractiveness may not have reflected the attractiveness to frugivorous birds, since we have seen birds eat shrivelled fruits of some plant species, particularly during late January and early February, when the availability of ripe fruits declines rapidly (Corlett 1993). Future studies need to investigate changes in fruit quality after ripening and follow the fates of fruits after they are shed from the plant.

The most interesting fruits in this persistence survey were *Alyxia sinensis* and *D. calycinum*, which have long persistence when bagged, but are removed rapidly when not bagged. These fruits appear to have effective antimicrobial defences that do not deter vertebrates. If these defences are chemical in nature, they could be of potential pharmaceutical interest. The long-persistent fruits of *P. tutcheri*, however, were unattractive to both microbes and frugivores, suggesting a more general toxicity.

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