

Floral biology of the distylous Mediterranean shrub *Jasminum fruticans* (Oleaceae)

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Various aspects of the reproductive biology of two populations of the distylous shrub *Jasminum fruticans* (Oleaceae) in the northwest Iberian Peninsula were studied during 1994 and 1995. This species is a 'tropical' relict of pre-Miocene origin. Two morphs (the L morph with long-style/short-stamen, and the S morph with short-style/long-stamen) occur. Our results indicate that morph frequency ratio in the study populations is one-to-one. Experimental crosses revealed self-incompatibility, very weak within-morph compatibility and strong between-morph compatibility (in all cases as is typical of distylous species). Pollen grains are larger in S-morph plants, while both nectar reward and fruit set are higher in L-morph plants. However, no differences were detected in number of pollen grains per stamen or in pollinator spectrum (the most frequent visitors to flowers of both morphs being species of the hymenopteran genera *Anthophora*, *Melecta* and *Bombus*).

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Introduction

Discrete sexual polymorphisms (i.e. dioecy and heterostyly) have always been of interest to plant ecologists, as models of the evolution of sexual systems and of reproductive strategies in general. Distyly is the existence within a single species of two floral morphs (long-stamens/short-pistil and short-stamens/long-pistil). In most distylous species, the two morphs are physiologically incompatible (Ganders 1979; Barrett 1992; Ornduff 1992). Distyly was probably the first plant breeding system to be analysed in evolutionary terms (Darwin 1877; see Bawa and Beach 1981). Specifically, Darwin proposed that distyly (i.e. reciprocal herkogamy) arose initially in response to selective forces increasing the accuracy of pollen transfer between individuals. This complex question has been hotly debated ever since (for review, see Lloyd and Webb 1992).

The morphs of distylous plants typically differ in various other respects, such as pollen size and pollen amount (see Ganders 1979; Dulberger 1992; Richards & Koptur 1993; Eckert & Barrett 1994). Both morphometric and functional differences may have important consequences for reproductive biology. For example, there have been reports of between-morph differences in number of grains of pollen removed from the anthers by insect visitors, and in the number of grains of pollen deposited on stigmas (Ganders 1979; Piper & Charlesworth 1986; Glover & Barrett 1986; Wolfe & Barrett 1989; Dulberger 1992; Stone & Thomson 1994). Differences of this type may imply between-morph fitness differences and, in the long term, shifts in the relative frequencies of each morph within the population (Charlesworth & Charlesworth 1979; Ornduff 1979; Barrett et al. 1989; Washitani et al. 1994; Arroyo & Dafni 1995; Eckert & Barrett 1995).

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In the present study we investigated various aspects of the floral biology of two populations of the distylous shrub *Jasminum fruticans* L. in the northwest Iberian Peninsula. Our general aim was to determine whether the floral biology of this species accords with that described for other distylous plants. More specifically, we aimed to identify possible between-morph differences in reproductive biology. To this end, we investigated a) flower characteristics (style length, stamen length, pollen production, pollen size), b) relative abundances of each morph in each population, c) morph compatibility (as revealed by hand pollination experiments) and d) nectar production by, and pollinator spectrums of, plants of the two morphs.

Natural history of the plant

The genus *Jasminum* (Oleaceae) is one of a group of 'tropical' genera (also including *Olea*, *Daphne*, *Rhamnus* and *Phillyrea*) which arose before the Miocene and which survived in southern Europe after the climate became Mediterranean (Raven 1973; Quezel 1985). Within this group, *Jasminum fruticans* is the only species known to display heterostyly Herrera 1984. It is an evergreen shrub with angular stems and trifoliate leaves. Vegetative reproduction is common. The flowers are yellow, about 15 mm long, with pistil protruding from the corolla and stamens enclosed within it (L morph) or with pistil enclosed and stamens protruding (S morph). Distyly was first described in this species by Dommée et al. (1992). The fruit is a globose black berry. In our study area, flowering starts in the first half of April and finishes in mid-June. The species is rare in northwest Iberia, and exists in scarce populations in limestone areas with holm oak woodland as dominant natural vegetation. The species' global distribution covers Southern Europe, North Africa and Southwest Asia (Fernández-Galiano 1987).

Methods

The study area

The two study populations are located in Covas and in Villaverde de la Abadía, in the El Bierzo region of northwest Spain, close to the border between the provinces of Orense and León. The geological substrate is limestone. Individuals of *Jasminum fruticans* occur singly in clearings in holm oak woodland, characterized by *Quercus rotundifolia*, *Pistacia terebinthus*, *Prunus mahaleb* and *Arbutus unedo*.

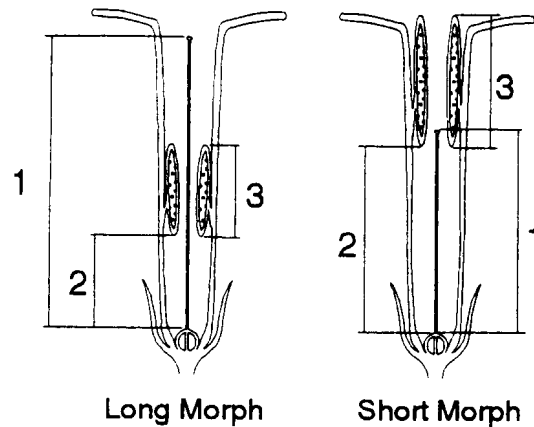


Fig. 1. Longitudinal section of a *Jasminum fruticans* flower, showing the morphometric characters determined (1 - style length, 2 - stamen filament length, 3 - anther length).

Experimental design

Floral biology was investigated in the Covas population in 1995. Flower duration was monitored during sunny periods by tagging 20 flowers (one from each of 10 plants of each morph), and visiting each plant every morning; observations of changes in the position of sexual organs were also made. To evaluate morphometric characteristics, 26 flowers (one from each of 13 plants of each morph) were collected and examined under a stereo microscope for measurement of style length, mean stamen filament length and mean anther length (Fig.1). The degree of 'reciprocity' of distyly was quantified with Eckert & Barrett's (1994) reciprocity index $RI = [L\text{-morph mean style length} - S\text{-morph mean stamen length}] / [S\text{-morph mean style length} - L\text{-morph mean stamen length}]$; stamen length was determined as filament length plus anther length. Eckert & Barrett's (1994) precision index $PI = [CV_L + CV_S] / 2$, where CV_L is the coefficient of variation in style length in morph L and CV_S the coefficient of variation in stamen length in morph S. An additional 20 flowers (one from each of 10 plants of each morph) were collected and stored in glacial acetic acid for subsequent determination of number of grains of pollen per stamen (in a Neubauer chamber as per Dafni (1992)). In addition, pollen from these flowers was mounted in 3:1 lactic acid-glycerin as per Kearns & Inouye (1993) for determination of mean maximum pollen grain diameter ($n = 160$ grains per morph) under an Olympus BX40 microscope with the aid of a Lupa SZ60 digital camera and Olympus WCUE image analysis software on a personal computer.

Morph frequency and female reproductive success

Morph frequencies were estimated on the basis of sampling along a randomly chosen transect in each population (55 plants in Covas, 40 plants in Villaverde) in April 1994. Each plant was tagged with coloured tape to prevent double-counting. These sample sizes are small a) because population sizes are small and b) because only clearly isolated plants were counted (to minimize bias due to spatial clustering of individuals of a clone). Fruit set in the Covas population in 1994 and 1995 was estimated in 15 plants of each morph (randomly selected from the 55 plants along the transect, and marked with metal tags) on the basis of counts of the total number of flowers and fruits produced by each plant.

Compatibility

To investigate self-compatibility and within- and between-morph compatibility, the following experiments were carried out in the Covas population in April 1995. First, four branches (one on each of two plants of each morph; 32 L-morph flowers, 23 S-morph flowers) were bagged with mosquito netting to prevent insect access. Second, 9 flowers on 4 L-morph plants and 16 flowers on 6 S-morph plants were individually bagged after brush pollination with pollen from the same flower. Third, 30 flowers on 5 L-morph plants and 34 flowers on 4 S-morph plants were emasculated and brush-pollinated with pollen from another plant of the same morph, and then bagged. Fourth, 28 flowers on 4 L-morph plants and 34 flowers on 4 S-morph plants were emasculated and brush-pollinated with pollen from another plant of the other morph, and then bagged. In all cases, fruit set was monitored after 4 - 5 weeks.

Nectar production

Sixty flowers (on 30 plants of each morph in the Covas population) were bagged on the day of the flowers opened for 24 h, and nectar volume in each flower was then determined with the aid of 2 or 10 μ l capillary micropipettes (Drummon Sci. Co.). Since flowers were bagged in the evening, when nectar is invariably entirely depleted, these determinations are a measure of nectar production over 24 h. Sugar concentration in nectar was determined with the aid of a portable refractometer (Bellingan and Stanley $\text{\textcircled{R}}$); the amount of sugar (mg per flower) and the energy investment (joules per flower) were then calculated by the method of Prys-Jones & Corbet (1978).

Pollination

Pollinator spectra were investigated in both populations, by monitoring visits to flowers of plants of each morph along the transects marked out for estimation of morph frequencies. Monitoring was done over 15-minute periods (total 5 h and 89 flower visits for L-morph plants; 5 h and 69 flower visits for S-morph plants). The results for the two populations were pooled. Specimens of all frequent visitors were captured and transferred to the laboratory to confirm identification.

Data analysis

Morphometric characteristics and nectar production/concentration were compared between morphs by *t* tests. Whether the relative frequencies of the two morphs differed significantly from one-to-one was investigated with *G* tests. Between-year and between-morph variation in fruit set were investigated by two-way analysis of variance. For the compatibility experiments, the effects of treatment (same-flower, other-plant/same-morph or other-plant/other-morph pollen) and morph on fruit set were investigated by logistic regression (subroutine CATMOD in the SAS package; SAS 1992); in this analysis, each flower is treated as an independent event with two possible outcomes ('set fruit' or 'did not set fruit'); parameter estimation is by a maximum likelihood method. Pollinator spectra of the two morphs were compared by a heterogeneity χ^2 test. Where sample distributions showed severe deviations from normality, percentage values were subjected to arc-sine transformations.

Results

Flower characteristics

Floral duration was 3 days for both morphs. Over this period, the positions of the sexual organs change. In S-morph flowers, the stamens move together at opening, blocking entry to the corolla; during the second and third day they gradually spread, permitting insect access. In L-morph flowers, the tip of the style is initially curved but later straightens out slightly.

Mean number of pollen grains per stamen was 5375 ± 1968 (\pm sd) for L-morph flowers and 5519 ± 2157 for S-morph flowers; these values do not differ significantly ($t = 0.16$, $df = 18$, $p = 0.88$). Mean maximum diameter of pollen grains was significantly higher for S-morph than for L-morph flowers (51.9 ± 4.4 μ m and 63.2 ± 3.1 μ m, for L and S morphs respectively; $F = 711.9$, $df = 1$, $p < 0.0001$). Clear differences were also observed in

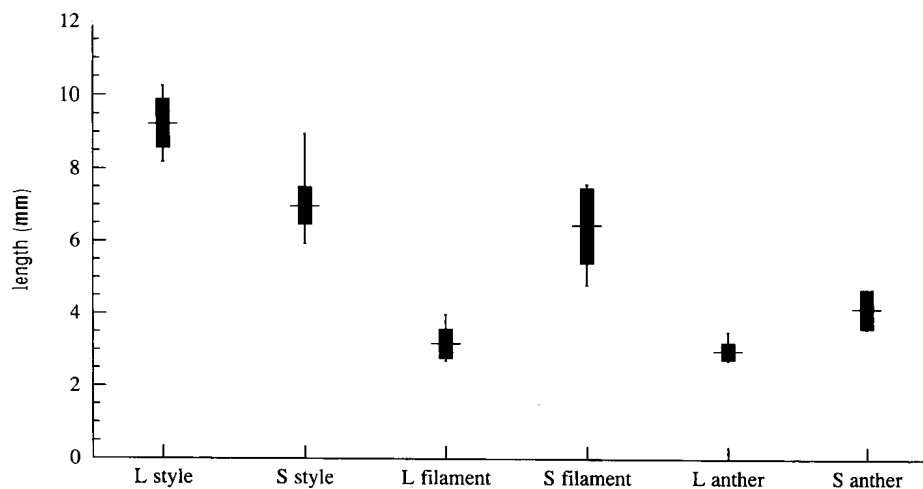


Fig. 2. Mean style length, stamen filament length and anther length in flowers of L- and S-morph individuals of *Jasminum fruticans*. Standard deviations and ranges are also shown.

other morphometric characteristics (Fig. 2): the ratio of L-morph style length to S-morph style length was about 1.3. The Eckert-Barrett reciprocity index was 0.5, and the Eckert-Barrett precision index 9.2 (CV for S-morph stamens = 11.5%, CV for L-morph styles 7.3%).

Morph frequency and fruit set

In the Covas population, 51% of plants sampled were L-morph and 49% S-morph. In the Villaverde population, 60% were L-morph and 40% S-morph. Neither distribution differs significantly from one-to-one (Covas - $G = 0.02$, $p = 0.89$; Villaverde - $G = 2.5$, $p = 0.11$).

Fruit set varied between 19.5% and 86.8% ($n = 60$, i.e. 30 plants in 1994 and 1995). Mean fruit set of L-morph plants ($51.6 \pm 17.6\%$) was higher than that of S-morph plants ($37.8 \pm 14.0\%$). Analysis of variance (Table 1) indicates that morph, but not year, had a significant effect ($p < 0.05$) on fruit set; the morph \times year interaction likewise had no significant effect, indicating that the effect of morph was consistent between the two years.

The results of bagging experiments showed that *J. fruticans* requires insect visits for pollination.

Table 1. Results of analysis of variance to investigate the effects of year (1994 or 1995) and morph (L or S) on fruit set in *Jasminum fruticans*.

Source	SS	DF	MS	F	p
Year	0.03	1	0.03	0.86	0.36
Morph	0.22	1	0.22	5.96	0.02
Year*Morph	0.03	1	0.03	0.72	0.40
Error	1.01	28	0.04		

Compatibility

The results of logistic regression indicate that pollen source, but not morph, has a significant effect on the probability of a flower setting fruit (Table 2). The non-significant p value associated with the likelihood ratio indicates that the global fit of the model is good, and thus that the pollen source \times morph interaction was not significant (i.e. the effect of treatment did not differ among morphs). All flowers were self-incompatible; within-morph compatibility was very low, while between-morph compatibility was high (Fig. 3).

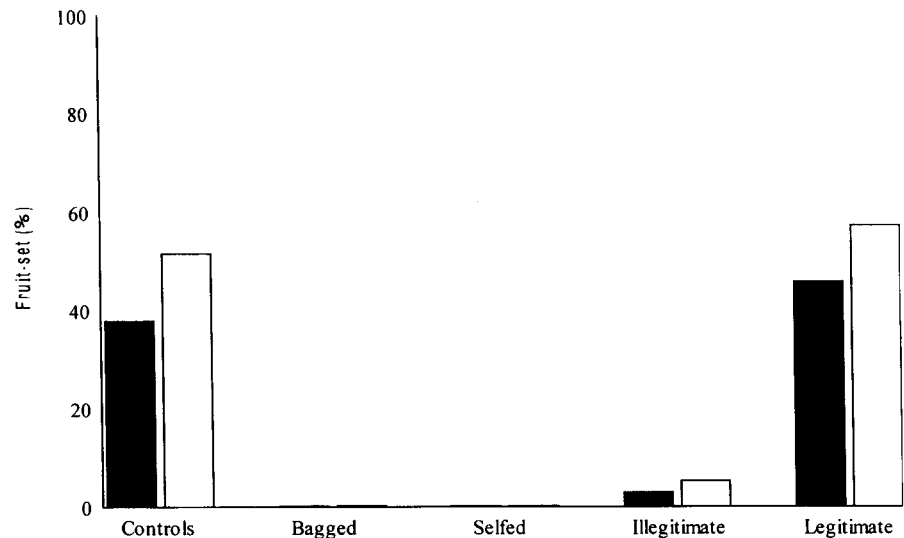
Nectar production and pollination

Both the 24-hour nectar production and sugar concentration of nectar differed significantly between the two morphs, and estimated per-flower investment in nectar was about 3.5 times higher in L-morph plants than in S-morph plants (Table 3). The most frequent visitors to flowers of both morphs were *Anthophora acervorum* and a *Melecta* species (Anthophoridae) and *Bombus pascuorum* (Apidae) (Table 4). The relative frequencies

Table 2. Results of logistic regression (see Methods) to investigate the effects of morph (L or S) and pollen source (same-plant, same-morph or other-morph) on the probability of a flower setting fruit. Note that the likelihood ratio is analogous to the residual sum of squares in linear regression.

	d.f.	χ^2	p
Morph	1	0.18	0.671
Treatment	3	37.7	0.000
Likelihood ratio	3	0.14	0.986

Fig. 3. Mean fruit set (%) of S- (black) and L-morph (white) flowers of *Jasminum fruticans*, a) pollinated naturally (controls), b) after bagging of flowers to prevent insect access, or after pollination with c) same-flower pollen, d) other-plant/same-morph ('illegitimate') pollen or e) other-plant/other-morph ('legitimate') pollen.



of visits by these three species did not differ significantly between the two morphs (heterogeneity $\chi^2 = 0.267$, $df = 2$, $p > 0.05$).

Discussion

Floral characteristics and female reproductive success

Our results confirm that flowers of the study populations of *Jasminum fruticans* are distylous, like other species of this genus (Ganders 1979): individual plants are either L-morph or S-morph. Both the L-to-S-morph style-length ratio (1.3) and the S-to-L-morph pollen-grain-diameter ratio (1.2) are within the ranges previously reported for distylous plants (Dulberger 1992). In distylous plants, pollen grain diameter is typically higher in the S-morph than in the L-morph. In most distylous plants, the L-morph produces more pollen grains per stamen than the S-morph (Ganders 1979); in our population of *J. fruticans*, however, number of pollen grains per stamen scarcely differed between the two morphs (5375 in L versus 5519 in S).

Eckert-Barrett indices of reciprocity and precision are likewise within the ranges reported for other heterostylous species (Eckert & Barrett 1994). Typically heterostylous species require insect visits for pollination; within-morph variation in the relative positions of the sexual organs (as measured by PI) may thus be expected to lead to appreciable among-individual variation in the efficiency of pollen donation and/or receipt (Ganders 1979).

Morph frequencies and female reproductive success

Most populations of distylous species have one-to-one morph frequency ratios (Dulberger 1992) as in the present study of *Jasminum fruticans*. In our study populations, L-morph plants had markedly higher fruit set (52%) than S-morph plants (38%) (though overall fruit set was similar to that reported for other fleshy-fruit-producing species (Stephenson 1981)). Similar patterns have been documented in numerous distylous species, and have been interpreted as a reflection of more efficient pollen receipt by L-morph flowers (Richards 1986). In view of the one-to-one morph frequency ratio, the higher fruit set of L-morph plants sug-

Table 3. Mean 24-hour nectar production of nectar (μl) and mean sugar concentration of nectar (mg ml^{-1}) in flowers of L-morph and S-morph individuals of *Jasminum fruticans*. Estimated per-flower investment (mg sugar) and per-flower energy investment (J) are also shown. Mean 24-hour production differed significantly between the two morphs ($t = 3.06$, $p = 0.0038$), as did mean sugar concentration ($t = 5.31$, $p < 0.0001$).

		L	S
Amount	μl	1.8 ± 0.7	0.4 ± 0.1
Concentration	mg ml^{-1}	27.6 ± 3.3	33 ± 4.3
Weight*	mg	0.435	0.121
Energetic content*	joules	6.78	1.86

* Estimated from means amounts and mean sugar concentrations

Table 4. Pollinator visits to L-morph and S-morph *Jasminum fruticans* flowers.

Species	L-morph n (%)	S-morph n (%)
Hymenoptera		
Apidae		
<i>Bombus terrestris</i>	3 (3.4)	1 (1.5)
<i>Bombus pascuorum</i>	4 (4.5)	8 (11.8)
<i>Apis mellifera</i>	-	1 (1.5)
Anthophoridae		
<i>Anthophora acervorum</i>	39 (43.8)	26 (38.2)
<i>Anthophora hispanica</i>	1 (1.1)	2 (3)
<i>Melecta</i> sp.	23 (25.8)	12 (17.6)
Andrenidae		
<i>Andrena</i> sp.	1 (1.1)	1 (1.5)
Megachilidae	1 (1.1)	5 (7.4)
<i>Osmia</i> sp.	3 (3.4)	4 (5.9)
<i>Megachile</i> sp.	1 (1.1)	5 (7.4)
Diptera		
Bombyliidae		
<i>Bombylius major</i>	4 (4.5)	1 (1.5)
Lepidoptera		
Papilionidae		
<i>Iphiclides podalirius</i>	6 (6.7)	1 (1.5)
Pieridae		
<i>Anthocharis bellia</i>	1 (1.1)	1 (1.5)
Sphingidae	1 (1.1)	-
<i>Hemaris fuciformis</i>	1 (1.1)	-

gests that some other components of reproductive success must be lower in this morph than in the S-morph. Candidate components include a) flower number, b) seed viability and/or seedling survival (Dommée et al. 1992), c) male function and d) asexual reproduction (Lovett-Doust 1989; Reekie 1991). Our results do not allow us to identify which of these factors is responsible in the present case. In a recent study of a *Lithospermum* species, between morph variation in fecundity was found to be attributable to variation in plant size (McCall 1996). L-morph individuals of *J. fruticans* invest more heavily in fruit production than S-morph individuals, and it seems reasonable to suppose that this will affect both vegetative reproduction (Reekie 1991) and size. In accordance with this, the lower fruit set in S-morph individuals might be compensated for by larger plant size.

Compatibility relationships and pollination

The plants of our study population of *Jasminum fruticans* are self-incompatible and shows very weak within-morph ('illegitimate') compatibility, as reported previously for this species by Dommée et al. (1992) and in accordance with the general rule for distylous species. Fruit set after 'legitimate' fertilization was similar to that observed in control (naturally pollinated) plants, suggesting that pollen limitation does not occur (or, at least, did not occur during the two years of study). We did not detect any appreciable between-morph difference in pollinator spectrum. The three most frequent visitors (all hymenopterans, and together accounting for about 70% of visits) are generalist pollinators of many tubular-corolla species present in this area (Gutián et al. 1994). Dommée et al. (1992), who studied a population of *J. fruticans* in southern France, found that the most frequent pollinator was a dipteran of the genus *Bombylius*.

Our results additionally indicate that nectar reward differs between the two morphs: 24-hour nectar production was higher but sugar concentration lower in L-morph flowers. The mean energy content of nectar in the two morphs indicates that per-flower investment in nectar by L-morph plants is about 3.6 times the investment by S-morph plants. Little information is available on nectar production by other distylous species (though see Arroyo and Dafni 1993). Our results as regards nectar production and pollen characteristics raise the possibility that the two morphs have two different pollination pathways, thus increasing flexibility in the face of environmental variability (Dommée et al. 1992; Björkman 1995).

In conclusion, the results of the present study indicate that the reproductive biology of *Jasminum fruticans* in most respects accords with the general pattern for heterostylous species. Pollen grains are smaller, while both fruit set and nectar reward are higher, in L-morph plants; however, we did not detect any between-morph differences in pollinator spectrum.

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Review

Vaughan, J. G. & Geissler, C. 1997. The new Oxford book of food plants. Oxford University Press. 239 pp. ISBN 0 19 854825 7. – GBP 25.

The “Oxford book of food plants” has been out of print for quite a long time, so it is welcome to see a new edition on the market. It is indeed a very much changed and enlarged book. The excellent illustrations by B. E. Nicholson are still the “backbone” of the book; it can only be said again that every plate is a masterpiece. Some new illustrations have been added by Elisabeth Dowle and Elizabeth Rice, e. g. a plate on pseudo-cereals: quinoa and buckwheat and “more legumes”: Tamarind, grass-pea, white lupin and guar (*Cyamopsis tetragonolobus*). The text is revised and updated throughout.

There is an introductory glossary of commonly used botanical terms, illustrated with small line drawings. This is followed by a short general chapter on domestication of food plants. In a paragraph on plant classification it is said that “in a perfect situation, a species should have one scientific name but sometimes an alternative name or synonym (syn.) is available”. This wording is unfortunate because a synonym is certainly not an alternative name.

The last 28 pages comprise a chapter headed: Nutrition and health. This gives a review of the food components: water, carbohydrates, fat, vitamins, minerals etc. There is also a part headed: Effects of processes and storage, and some tables covering the compositions of some major groups of commodities e. g. grains and cereals, oil seeds and fruits, legumes, fruit and vegetables. Finally there is a list of recommended reading. This only gives English language books, some of the most comprehensive works in other languages being regrettably omitted e.g. Heinz Brücher, Tropische

Nutzpflanzen, 529 pp., (1977). Another German book that the reviewer misses has even been translated into English: S. Rehm & G. Espig: The cultivated plants of the tropics and subtropics, 552 pp., with a literature list of no less than 2 033 titles. All in all the book is very English, particularly when it comes to horticultural varieties of e. g. potatoes, apples and pears, where only cultivars grown in Britain are mentioned and illustrated. Nothing wrong about that of course, but the reader should bear it in mind.

Many new, particularly tropical, fruits and vegetables have been introduced to the Temperate market in recent decades, and not all of them have found their way into the new Oxford book. It is mentioned that pepino, *Solanum muricatum*, has been introduced to countries such as Morocco, Spain, Israel, Kenya and New Zealand. The reviewer is fairly certain that it also occurs in Britain; it was in fact brought to France in 1785 and to the U. S. A. in 1882, where it was called “Melon Pear”: it is often seen in the supermarkets in Denmark.

Under *Lepidium sativum* on page 162 it is said that “cress seedlings may be included in “mustard and cress”. Seedlings are indeed popular today, and many “kinds” can be bought throughout Europe, so why not mention *Medicago sativa*, which are among the more commonly sold ones? Under *Taraxacum officinale*, in the chapter on Coffee, it is mentioned that in continental Europe the leaves are used in salads and the inflorescence for making wine. This is hard to believe, and in any case real wine can only be made from grapes. *Valerianella olitoria* is also missing.

In spite of its very “Englishness” this is a handy and useful book, not only for college student but for everyone interested in food plants in their widest sense: they are indeed one of the most important factors in our daily life.

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