

## *Kandelia candel* and '*Kandelia obovata*'; ecotypes, varieties or different species?

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**Abstract:** Recently there has been an attempt to subdivide *Kandelia candel*, a long established Rhizophoracean mangrove species, into two species: the existing *Kandelia candel* and '*Kandelia obovata*' described as a 'new mangrove species from Eastern Asia'. While many in mangrove science will welcome additions to biodiversity, especially at the higher plant level of taxonomy, this paper sounds a cautionary note as it critically examines the taxonomic and ecological basis for the attempted creation of *Kandelia obovata*. Special attention is given to ecophysiological adaptations within various populations of *Kandelia candel* such as cold tolerance and to a number of morphological and anatomical leaf and flower attributes which can be found throughout the biogeographic range of this species. Comparisons are made with another well known, widely dispersed and cold tolerant species, *Avicennia marina*, to illustrate the important taxonomic point that polytypicity in terms of subspecies within species is the norm rather than the exception. The paper concludes by strongly contending that *Kandelia candel*, at present, consists of two ecotypes which may be indicative of subspeciation within the existing gene-pool of *Kandelia candel*. Thus the 'new' *Kandelia* species, '*Kandelia obovata*' is at the very least premature and should be looked upon as no more than an ecotype with, perhaps, subspecific potentialities.

**Keywords:** *Kandelia candel*, *Kandelia obovata*, *Avicennia marina*, intraspecific variation, ecotypes, subspecies, gene-pools, reproductive isolation.

### Introduction

This paper reviews what is and is not known about the taxonomy, ecology and ecobiogeography of *Kandelia candel* (L.) Druce, long regarded as a monotypic species within the Rhizophoraceae (Yamashiro, 1961; Wang *et al.*, 1964; Nakasuga *et al.*, 1974; Chapman, 1976; Ho, 1980; Nakamura, 1982; Hu *et al.*, 1986; Tomlinson, 1986; Chen *et al.*, 1988; Maxwell, 1993 and Chang, 1997).

In recent years the field of mangrove genetics has gained a new spark of activity which should be welcomed. On close examination of the resultant publications in mangrove genetics and biodiversity, it can be seen that these studies appear to be based on a relatively small percentage of the total genome available within the species populations studied. This situation is also the case with the widely dispersed (Chapman 1975; Tomlinson, 1986; Urasaki *et al.*, 1986; Maxwell 1993, 1995; Chiang *et al.*, 2001 and Chiou-Rony Shew *et al.*, 2003) and rather understudied mangrove, *Kandelia candel* (Aksonkoae *et al.* 1992, Maxwell, 1993, 1995, Maxwell *et al.*, 1997). In areas where *Kandelia candel* is a relatively conspicuous member of the mangrove community, this species features more strongly in the literature, e.g. in Japan, China and Hong Kong. Japanese botanists and ecologists have a long history of *Kandelia* studies (as evidenced in my recent inspection of the impressive collection of *K. candel* herbarium material held at Tokyo National Science

Museum, covering the period 1896 – 1970; TNS 2000). Perhaps one of the neatest and core studies being that of Yamashiro (1961) on propagule dispersal, a theme picked up again by Nishihira & Urasaki (1983) and Urasaki *et al.* (1986). In China, *Kandelia candel* features in ecological studies which often relate to economic utilization of mangroves but also include observations on cold tolerance and ecotypicizing e.g. Lin & Fu (2000). Likewise, in Hong Kong where mangrove science has recently become a more popular topic for research, *Kandelia candel* has been long recognized as a conspicuous species within the eight or nine true mangroves which occur here (e.g. see reviews by Hodgkiss, 1986 and Maxwell, 1993). In Japan, China and Hong Kong, one of the outstanding attributes of *K. candel* which has gained the attention of botanical scientists, is cold tolerance (Maxwell, 1995; Maxwell *et al.*, 1997). While this point has interested Japanese scientists (e.g. Sakai, 1974; Nakamura, 1982; Nakagoshi & Nehira, 1986) for decades, it has typically escaped the attention of many others and the idea that the only mangrove species to exhibit cold tolerance is *Avicennia marina* is still widespread in the literature (e.g. Duke *et al.* 1998 and Kathiresan & Bingham, 2001). Happily, Saenger (2002) citing Maxwell (1995) may help to correct this false impression.

The attribute of cold or chill tolerance has very important biogeographic implications. It is surprising therefore to find *Kandelia candel* as being totally ignored

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in reviews of global mangrove spatial issues (e.g. Farnsworth, 1998) and responses to environmental change & stress (e.g. Kathiresan & Bingham 2001). This may reflect at least in part, the tendency to pay little attention to what is perceived to be 'regional' literature rather than 'international' literature: a trend which is unfortunate in modern ecological writing. The publishing trend, encouraged by universities seduced by so called 'impact factor' thinking about scientific literature, works against what is perceived as locally and regionally relevant publishing and publications. Consequently, some important ideas are ignored by writers attracted to so-called 'high impact', 'international journals' (Maxwell, 1998).

My objectives in this paper are to discuss many important issues which, in my earnest assessment, should be fully addressed *before* biologists (of all disciplines and sub-disciplines) accept the taxonomic validity of *Kandelia obovata*, as a new species. My paper aims to show that, at present, it is far more acceptable to give due recognition to at least the ecotypes within the *K. candel* species population and, at most, the possible subspecies or varieties of *K. candel*.

The paper begins with some important general biological and taxonomic issues and then moves on to more specific aspects of some recent trends in mangrove thinking in genetics and evolution. My paper attempts to evaluate these trends and presents a conclusion that *K. candel* is yet another example, like *Avicennia marina* (Tomlinson, 1986; Everett, 1994) and *Excoecaria agallocha* (Parani *et al.*, 1997) of strong ecotypicity and genetic polymorphism within the mangrove flora. In style, the paper in its present form and organization is designed as a 'lecture on paper'.

## 1. The species concept and polytypicity

The concept of reproductive isolation or genetically isolated gene pools is still, I believe, a core component of the species definition. Likewise, the concept of gene pool as the sum total of all genes in an interbreeding population remains essential in population genetics (Thain & Hickman, 2000). It is possible that within biology, zoologists are perhaps more strongly attracted to the core concept of reproductive isolation in defining a biological species. The nomenclature of the Iriomote cat is an excellent case in point here! There are those, too, who feel that because it may be hard to define a species; to list the necessary properties for this biological taxon, that we should be relaxed and flexible about the 109 process of species taxonomy. Yet, as Thain & Hickman (2000)

argue, we still need to define a species in philosophical terms even if this is not always so easy. The word species is not equivalent to element or compound in scientific status. Nevertheless, despite this lack of precision, we in biology should not create new species too easily, especially if the core evidence for reproductive isolation is lacking. As Thain and Hickmott (2000) remind us, most species probably comprise two or more subspecies or races and are said to be polytypic. *Bos domestica* consists of 6-8 major breeds each with numerous morphologies and biochemical differences but are still one species. Likewise, with *Canis familiaris* (the domestic dog).

Finally, who, in anthropological circles, would welcome a proliferation of new species designations for the very polytypic species, *Homo sapiens*? There would even be justified resistance to the use of subspecies with respect to *H. sapiens*.

## 2. Some sources of uncertainty in mangrove taxonomy

### 2.1 Hybridization

As Duke (1992) pointed out, many problems still exist with mangrove taxonomy and many of these are based on hybridization between species (Kathiresan & Bingham, 2001). Let it be emphasized here too, that this idea is not new and has been noted by mangrove field botanists before Duke (1992) or Kathiresan and Bingham (2001), e.g. by Nakamura (1982) who wisely remarked that it can be difficult to always easily distinguish *Rhizophora mucronata* in Thailand from (*R. stylosa* in Japan. Nakamura pointed out that a careful examination of the style may be necessary. *R. stylosa* typically has a long style). Debate continues on the number of species. Tomlinson (1986) lists 54 species, while Duke (1992) and Field (1996) accept 69. Sun *et al* (1998) prefer ~ 80 spp. Lin & Fu (2000) settle on 70; Kathiresan & Bingham (2001) 'reconcile' the figures of Tomlinson (1986) and Duke (1992) to get 65 species and finally, Primavera *et al.* (2004) diplomatically embrace the flexible number of "around 70". Who are we to believe? Clearly, more work needs to be done and if *Kandelia obovata* is to be accepted as a valid species, the number will again increase by one 'new' species. Will the new revised number be 55, 70, 71, 66 or 81?

Clearly Duke (1992) was correct in identifying problems and some of these may stem from hybridization. The matter is dynamic and in a state of flux. An excellent example of this flux comes from the dynamic status fluctuation of *Rhizophora annamalayana* from southern India. Kathiresan (1995) described *R. annamalayana* as a 'new' species. But recently Snengor (2002) citing Parani *et*

**Table 1** Variation in leaf features in *E. agallocha* and *E. ovalis* from Australia (based on the above paper)

Species (geography)	length	Width	Petiole	Margin	Apex
<i>E. agallocha</i> (NSW)	71.2±10.0	40.7±7.7	14.6±2.9	crenate	Blunt-acute
<i>E. ovalis</i> (WA)	39.3±2.1	25.3±2.5	11.3±1.2	Entire	Blunt

al. (1997) who used some genomic DNA analysis, argued that this 'new' *Rhizophora* species was (only) a sterile F<sub>1</sub> hybrid of *R. mucronata* and *R. apiculata*.

In similar studies, *R. lamarckii* was viewed as the hybrid between *R. apiculata* and *R. stylosa* (Tomlinson *et al.*, 1979). As Nakamura (1982) showed, some careful field work with actual populations can help botanists to avoid making mistakes or conducting incomplete studies.

Saenger (2002) wisely concludes, I believe, that although hybrids are also known within the species associated with *Sonneratia*, *Xylocarpus* and *Lumnitzera* as well as *Rhizophora*, this hybridization should be taken to indicate that the genetic isolation between species of these genera are not complete. And, let it be emphasized, these mangrove genera are of outstanding importance within global mangrove flora. Thus, I contend, we should adopt a conservative approach when contemplating 'new' species within mangrove genera, including *Kandelia*.

## 2.2 Molecular or microgenetic variations

In recent years, a new field of ecology has caught the imagination of a number of workers; it is *molecular ecology* and molecular genetics a source of many tools within this field. Molecular genetic techniques are helping to shed new light on ancestry and evolutionary connection of mangrove species (Saenger, 2002). I will now examine some case studies in molecular genetics of mangroves and show that, although interesting, these innovative contributions rarely prove the existence of new species.

### 2.2.1 Use of *Internal transcribed spaces* (ITS) region of *ribosomal genes* (Maguire & Saenger, 2000) with *Excoecaria* spp.

This work was done with geographically isolated populations of *Excoecaria* from New South Wales, Western Australia and Queensland and showed that the various *Excoecaria* species, *E. agallocha* (E. Aus, i.e. New South Wales) and *E. ovalis* (from W. Australia) were genetically uniform within species but differed from each other consistently. Leaf morphology especially length, width, petiole, margin and apex also varied (Table 1).

*E. ovalis* has only recently been elevated to species status on the basis of morphological (Wightman, 1989) and DNA (Maguire & Saenger 2000) data.

But, I ask, two questions here:

(1) How much of the total genome was represented by the ITS regions of ribosomal genes? and

(2) Were reproductive compatibility (cross-fertilization) tests done on these two 'species' of *Excoecaria*?

If they are not genetically isolated, then is *E. ovalis* really a separate species from *E. agallocha*?

Is *E. ovalis* a subspecies of *E. agallocha* i.e., *E. agallocha* var. *ovalis*?

### 2.2.2 Chemotypicity i.e. 'chemotypes' in *Rhizophora mangle* and *Avicennia germinans*

Kathiresan & Bringham (2001) cite the work on *Rhizophora mangle* from Puerto Rico which indicated the existence of 'distinct chemotypes' within this American *Rhizophora* species (Corredor *et al.*, 1995). On close study of the original paper by the Corredor group, it is clear that work is restricted to albino mutants, which in nature have a chance of short term survival largely due to vivipary. I report similar observations with *Avicennia marina* var. *resinifera* in New Zealand. Here they were not albinos but rather, yellow mutants, clearly deficient in chlorophylls (Maxwell, 1971). They lasted as long as the food store in fleshy cotyledons; clearly they were not part of a future gene pool.

While these 'pigment Fingerprints of chlorophyll deficient mutants' are interesting, they are simply mutants. The term, chemotype, does in my view hint at a status closer to that of ecotype. The term ecotype implies much more than mutation around several different loci, as was the case with these *Rhizophora mangle* heterozygotes. I feel, therefore, that the term chemotype conveys far more taxonomic meaning than it should and contend that the use of this term in the context of an account of genetic variation within mangroves is misleading.

### 2.2.3 'Ecotypic diversity' in cuticular waxes of mangroves at 'the bioclimatic extreme'

Again Kathiresan & Bingham (2001) discuss foliar leaf waxes as evidence of genetic variation within mangroves. I accept that this is an example of such variation but do not accept the implication, conveyed in the above title to the paper by Dodd *et al.* (1999), that this can be interpreted as subspeciation or even ecotypicity in action.

In addition, while the mangrove species that can occupy 'one of the direst habitats in the world', *Avicennia marina*, is at a bioclimatic extreme, it is not at 'the bioclimatic extreme'. There are other such bioclimatic extremes including the northern limit of *Kandelia candel*, in Japan and the southern limit of *Avicennia marina*, at Ohiwa in New Zealand.

These developments in cuticular wax hydrocarbons (C33 & C31 long chain compounds) reported by Dodd et al (1999) are excellent examples in my view, of the inherent ecological plasticity that typifies *Avicennia marina*. They are not examples of evolution of new varieties or subspeciation.

#### 2.2.4 Isozyme studies in *Kandelia candel* populations

Studies by Sun et al. (1998) using isozyme electrophoresis on flower buds or youngest leaf buds of *K. candel* from 13 isolated microgeographic populations within the territory of Hong Kong, revealed little genetic variation among these populations. The actual percentage of total *K. candel* genotype (gene load) studied was very small e.g. heterozygosities observed and expected were calculated only for two common polymorphic allozyme loci.

The significance of these studies seems to point to conservative gene flow in *Kandelia candel*, a property which may be linked to its so far incompletely studied mating system. As indicated earlier by Baba et al (1989) isozyme genotype analysis could be an effective tool in mangrove species studies but care is needed and questions such as seasonal change of isozyme phenotype patterns should also be studied.

#### 2.2.5 *Kandelia candel* genetics in East Asian populations of this species.

Using nucleotide variation of chloroplast and mitochondrial DNA extracts from *K. candel* in Japanese islands, Taiwan, mainland China, East Malaysia and southern Thailand, Chiang et al. (2001) found significant gene allele differences in cp-DNA & mt-DNA in the northern and southern reaches of the South China Sea, but these differences did not lead these workers to proposed even a new subspecies and certainly not a new species form these *Kandelia candel* populations. They did show however, that some long-range seedling dispersal was evident. This finding tends to support the idea that *K. candel* produces propagules, some of which retain buoyancy for months, are capable of distant phytogeographic dispersals (Maxwell, 1993; Maxwell, 2002a).

#### 2.2.6 Inconsistent elevations of mangrove species to species status

This point is potentially huge; a paper or lecture in itself. In addition to the examples mentioned above, there are many others of which the following illustrate important aspects of the nature of these inconsistent treatments:

- (a) *Heritiera littoralis* and *H. fomes*
- (b) *Acrostichum aureum* ecomorphs
- (c) *Avicennia marina* subspecies, and
- (d) *Kandelia candel* vs. *K. obovata*

Each example will be addressed in turn.

##### 2.2.6.1 *Heritiera littoralis* and *H. fomes*

Accounts of these two species of mangroves within the Sterculiaceae by Saenger (2002), Das et al. (2001) and Tomlinson (1986) give overlapping but not identical assessments of the validity of these two species of mangrove *Heritiera*. Other botanists too, point to variations with *H. littoralis* populations especially in leaf morphology (e.g. Aksonkoe et al., 1992). The recent work by Das et al. (2001) using random amplified polymorphic DNA (RAPD) studies of *H. littoralis* and *H. fomes* has shown that the two species are closely related with a high level of intraspecific polymorphism. Tomlinson (1986) highlights the differences in fruit morphology as the key to specific subdivision in these two species: *H. littoralis* having a smooth fruit with 'a rudderlike crest' but lacking the transverse, circular ridge while *H. fomes* has a knobby fruit with a ventral ridge and a transverse circular ridge. It is possible too, according to Tomlinson (1986) that the ability or otherwise to produce pneumatophores (*H. fomes* can, but *H. littoralis* can't) may also separate these two species. In my assessment, more field work needs to be done and some close attention give to the core question of interfertility testing: are these two species of *Heritiera* completely isolated genetically?

##### 2.2.6.2 *Acrostichum aureum* ecomorphs

Ecomorphs or perhaps more genetically fixed growth forms have been reported within this species of mangrove fern (Medina et al., 1990). The work by the Medina team was done in Puerto Rico and their findings together with those of Lloyd and Buckley (1986) and Watson's (1928) observation in Malaysia point towards ecotypic differentiation, especially with respect to salt tolerance within *A. aureum* populations. This aspect of ecotypicity and the colourmorphs noted by Tomlinson (1986) i.e. S.E. Asian *A. aureum* young fronds having a characteristic crimson colour which is lacking in New

**Table 2** Mean measurements with standard error and ranges (in parenthesis below mean of numeric morphological attributes in populations of *Kandelia candel* from Brunei, Hong Kong and Thailand. Attributes 1-5 and 7-8 in cm; attributes 9 and 10 in g. (Ranges in brackets)

Attribute	<i>K. candel</i> populations				
	Brunei Tutong R.	Hong Kong Chek Keng	(MaiPo)DeepBay	Thailand La-Un	
(a)	Leaf				
1	Length L	11.8±0.124 (10.00-15.00)	6.69±0.11	9.11±0.131 (7.6-13.6)	15.00±0.11
2	Width W	3.48±0.032 (2.8-4.2)	2.80±0.06	3.9±0.064 (2.9-5.5)	6.23±0.06
3	Petiole length	1.01±0.04	0.71±0.01	1.20±0.016	1.29±0.03 (0.8-1.5)
4	L/W	3.41±0.44 (2.61-5.07)	2.40±0.039 (1.97-3.02)	2.45±0.024 (2.06-3.01)	2.63±0.02
5	L x W	20.65±0.332 (12.76-39.00)	9.56±0.341 (2.97-13.80)	17.89±0.570 (11.4-37.4)	50.61±0.692 (33.8-65.36)
6	General form	oblong-elliptic with some marginal curling	oblong- elliptic	oblong-elliptic	Broadly oblong- elliptic
(b)	Propagule				
7	Length	31.05±0.30 (18.9-39.5)	19.32±0.236 (10.9-27.0)	22.10±0.291 (14.8-27.95)	46.89±0.602 (40.2-53.6)
8	Width	0.95±0.006 (0.7-1.09)	1.09±0.114 (0.7-1.5)	1.30±0.009 (0.99-1.49)	1.32±0.012 (1.12-1.42)
9	Wet weight	15.67±0.399 (8.22-20.77)	9.83±0.265 (5.17-15.64)	14.72±0.288 (5.75-21.09)	34.37±1.193 (22.15-47.85)
10	Dry weight	6.76±0.13 (3.8-10.0)	3.26±0.251 (1.96-5.57)	7.19±0.168 (3.99-10.63)	12.87±1.465 (8.41-13.40)

(Adapted from Maxwell, 1995) (Means were subject to one-day ANOVA and post-test Bonferroni corrections. In all cases, except petiole length & width between Mai Po and La-Un the differences were significant (P=0.001 level))

World representative of this species.

Despite these differences and the all important ecophysiological difference in gametophyte tolerance of salinity that exists within various *A. aureum* ecotypes, there has been no serious attempt to date to subdivide *A. aureum* even into subspecies.

### 2.2.6.3 *Avicennia marina* subspecies

Varieties or subspecies within the worlds most widely dispersed and ecologically versatile mangrove, *Avicennia marina*, have been acknowledged and accepted as useful taxonomic categories for decades. Tomlinson (1986) address this taxonomic variation and cautions that morphological distinctions may not be clear cut. He nevertheless highlights some of the most distinctive features which do give at least some of these subspecies a

stamp of uniqueness. Likewise, Aksornkone *et al.* (1992) draw strong attention to the varieties within this species. In my extensive work on and with *A. marina* populations from the geographic southern limit in New Zealand (38 ° South at Ohiwa) throughout East and S.E. Asia, I have seen consistent differences especially between *A. marina* var. *resinifera* (NZ subspecies) and those of Hong Kong, Thailand and North Borneo (Brunei) (Maxwell 1971, 1993). Those from Thailand and Brunei fit the *A. marina* var. *marina* designations, while those of Hong Kong being dwarf with small stature, small leaves and small fruits strongly resemble those of Iriomote Island, Okinawa Prefecture, Japan. (Maxwell per obs, 2005). Despite true tropical condition in Iriomote and the absence of chill shock that is a feature of a Hong Kong winter (Maxwell, 1993, 1995, 2002,b) *A. marina* here assumes a consistent

**Table 3** *K. obovata* vs. *K. candel* (Vietnam work, extracted from Nguyen 2004 in Hong 2004 pages 163-173).

Feature	<i>K. obovata</i> ( <i>K.o.</i> )	<i>K. candel</i> ( <i>K.c.</i> )
1. stigma	3-lobed (more-closed)	3-lobed (more open)
2. cotyledons	More concave	More pointed
3. Propagule length	Shorter than <i>K.c.</i>	Longer than <i>K.o.</i>
	(no figures were given)	
4. Propagule cortex parenchyma	Smaller air spaces between cells	Larger air spaces between cells
	(no measurements were given)	

**Table 4.** Gene mutations and their taxonomic impacts in mangrove evolution (Adapted from Kathiresan and Bingham (2001) based on Saenger (1998))

# of gene mutations	Status/taxonomic or evolutionary impact
1-2	Minor biochemical differences e.g. albino mutants
5-10	Some change at the physiological level e.g. cold tolerance?
>10	Morphological variations e.g. leaf form
>100	Taxonomic change e.g. new subspecies, species

squat, sprawling growth form which is in stark contrast to the more erect trunk based architecture of non *Avicennia* mangrove species on Iriomote. It is possible that we have a new subspecies here. *A. marina* var. *iriomotensis*?

The acceptance of subspecies within the diverse *A. marina* species populations seems well established and was formalized again by Everett (1994) according to Saenger (2002).

While a comprehensive account of subspeciation within *A. marina* is possible, it is well beyond the scope of this paper. The central point, I wish to emphasise in the context of this paper on *Kandelia candel* vs. *K. obovata*, is that the acceptance of 5-7 subspecies within *A. marina* while not applying similar taxonomic thinking to *Kandelia candel* is inconsistent and unacceptable.

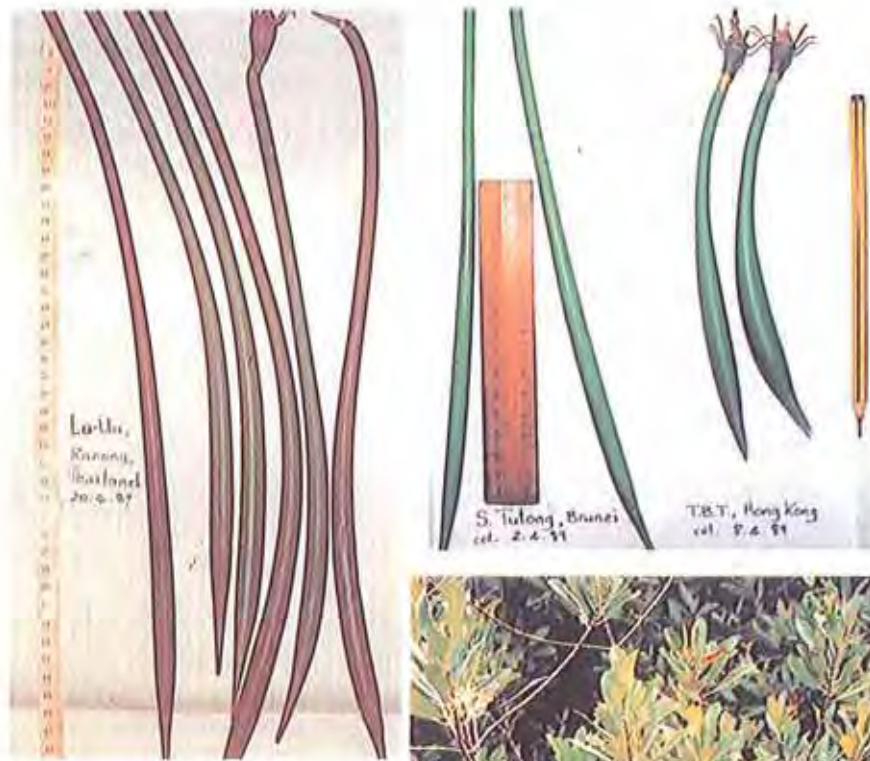
#### 2.2.6.4 *Kandelia candel* vs *K. obovata*

My work on ecogeographic variation within *Kandelia candel* population was the first, as far as I know, to report distinct ecotypes within this widely dispersed species (Maxwell, 1993; 1995).

These ecotypes are perhaps most readily seen in propagule morphology, a diagnostic attribute highlighted by Aksornkoac *et al.* (1992). (Photo 1) Other attributes included leaf morphology and interestingly, physiological differences in cold tolerance. Table 2 presents a summary of this study on ecotypicity (Maxwell, 1995). The work of Chiou Rong *et al.* (2003) builds on this data. Again there is an emphasis on what I would describe as interesting but minor, mostly non-reproductive characters. Examples

included, as one would expect, leaf shape, stipule length, sepal colour and size, petal and style size all of which strongly overlap. The main difference lies in hypocotyl length; with *K. candel* having 20-40cm long hypocotyls while those of '*K. obovata*' were smaller, at 15-23cm in length. No tests of statistical significance of the differences addressed were given in the Chiou Rong *et al.* (2003) paper announcing *K. obovata* as 'a new mangrove species'. Indeed, caution should be exercised even with these apparently strong propagule differences as shown by Maxwell (1995) (See Table 2 and photo 1). In a follow up study within Hong Kong Maxwell and Chope (1995) confirmed that propagule length can vary and be statistically significant, even within geographically isolated Hong Kong populations; these variations seemed to be ecological with perhaps hints of genetic isolation. Again we found the trend evident in Table 2, that morphological factors such as leaf and propagule size can vary markedly from site to site (e.g. Chek Keng vs. Mai Po within Hong Kong). It is noteworthy that the Mai Po *K. candel* growth attributes are similar to tropical Bruncian and Thai populations in several respects while those from Chek Keng are rather different in most respects (Table 2). The outstanding differences between Mai Po and Chek Keng are ecological: the Mai Po environment is characterized by soft, deep estuarine mud and lower salinities (~20ppt) while that of Chek Keng has a stony substratum with limited mud and high, salinities (~30ppt).

These studies tend to be in concert with those of Sun *et al.* (1998) and Chiang *et al.* (2001), mentioned above.



***Kandelia candel***

รังกะแท้



Photo 1. *Kandelia candel* by Aksornkoae et al. (1992).

Interestingly too, my recent inspection of the substantial collection of *Kandelia candel* herbarium material held at National Science Museum (TNS) illustrates such

variation (TNS, 2006). The sample pool provided by the TNS spans the East China Sea region throughout the Japanese islands and Taiwan, representing a wide range of

climate extremes and habitats. A systemic documentation of this TNS *Kandelia candel* resource is the subject of a future paper.

There was no intention to propose the formation of a new species, *K. obovata* based on ecotypes. Indeed, my work with transplantation, where seedlings of *Kandelia candel* ecotypes from Brunei and Thailand were grown to maturity in the same habitat at Hong Kong alongside local (Hong Kong) ecotypes indicated that they retained much in common. This was especially evident after a setting in phase of about five years, as the tropical transplants adjusted to the Hong Kong environment. All displayed some degree but not identical chill tolerance. Although there was more initial die back and mortality from cold ( $\sim 4^{\circ}\text{C}$  for 2-3 nights) with the tropical (Thai & Brunei) saplings than those from Hong Kong, representations of all ecotypes survived Hong Kong winters.

Furthermore and of paramount importance in my view, is the fact that today, some 15 years after the Hong Kong transplant field experiment was initiated, this group of three ecotypes are interfertile: there is no overt evidence of genetic or reproductive isolation! (Maxwell, pers obs 2004). This viewpoint appears to stand in contrast to the treatment of *Kandelia candel* populations in Vietnam as given by Nguyen (2004). Here some relatively minor morphological and anatomical differences with *Kandelia candel* populations are used to support the notion of two species; *Kandelia candel* and *K. obovata*. Table 3 presents a summary of this Vietnam work.

Chiou Rong *et al.* (2003) also present data on chromosome number which suggests that *Kandelia candel* has a  $2n$  chromosome number of 38 (Das *et al.* 1995) while '*K. obovata*' has 36 (Yoshioka *et al.*, 1984). This could be deemed important as Nguyen (2004) contends. However, the retention of ecotypic interfertility as mentioned above (2.2.7.4) within the three ecotypes of *Kandelia candel* (Maxwell, 1995) tends to cast a shadow of uncertainty over these chromosome numerical differences and moreover, if they do exist, their importance as isolation mechanisms. It will wise too, to consider and determine just how many gene mutations are needed before we can justify a taxonomic change at the species level. Kathiresan and Bingham (2001) who cite Saenger (1998) estimate more than 100 (Table 4). The work of Chiou Rong *et al.* (2003) and similar studies does not address this question nor the co-lateral issues of individual gene importance within the total genome, polygenic inheritance and nature and status of genes controlling genetic compatibility. Interestingly, the advocates of *K. obovata* as a 'new' species seem to ignore both the core

criterion of ecotypic interfertility (genetic compatibility) and such related considerations as numbers of mutations required for speciation in *Kandelia candel*.

### 3. How strong is the evidence used to justify subdividing *K. obovata* form *K. candel*:

Clearly, there are differences within this widely dispersed East Asiatic mangrove species known as *Kandelia candel*.

These differences are mostly minor morphological in nature. Both *K. candel* and the proposed *K. obovata* display cold tolerance. This propensity was also evident in the three ecotypes of *K. candel* investigated in transplant field experiments by Maxwell (1995). The differences in cold tolerance between the tropical (Brunei & Thai), *K. candel* ecotypes and the Hong Kong ecotype were strongest only within the first 5 years of the field trial and, today, are not so obvious.

Minor differences in leaf and inflorescences do exist with *K. candel* ecotypes. The same pattern is also displayed by the varieties of *Avicennia marina*. Excellent examples come from *A. marina* var. *resinifera* which has a more compact inflorescence than *A. marina* var. *marina*; larger leaves, a more acute apex, larger fruits, different buoyancy properties in the propagule and considerable cold tolerance not found in the more tropical subspecies. Recent work by Ge *et al.* (1999) using material from New Zealand, Hong Kong, China and Thai populations of *A. marina* has confirmed genetic divergence at the isozyme and chlorophyll-DNA levels. There is however, no suggestion of proposing new species for all these *A. marina* varieties or subspecies!

During my recent (Sept-November, 2006) field work on Iriomote island, Okinawa Prefecture (Japan), I was able to examine two growth forms of *Kandelia candel* which co-exist in the same habitat (Urauchi River mouth zone). The growth forms are distinct: one is a compact, squat, sprawling bonsai-like shrub with limited vertical trunk development; the other is a tree form. The possibility of some genetic basis exists (Baba, pers. Comm., TBRC, Univ. of Ryukyus) and these alternative growth forms of *K. candel* from Iriomote will be the subject of another paper. Field observations of this nature should be exhaustively studied to determine the ecological, climatic (e.g. typhoon patterns) and genetic (if any) basis of such biological variation. These recent observations tend to deepen my belief in ecotypicity and ecological plasticity within the gene pools of species such as *Kandelia candel* and *Avicennia marina*.



#### 4. Conclusion

I conclude by strongly advocating that the so called 'new' species *Kandelia obovata* be reviewed and re-designated as either an ecotype or, at most, a subspecies of *Kandelia candel*: perhaps, *K. candel* var. *obovata*. The other *Kandelia candel* populations could perhaps retain the original name and be known as *K. candel* var. *candel* or *K. candel* var. *macrocotyla*, a reference to the longer cotyledons! To date, in my assessment of biodiversity within the various populations of *Kandelia candel*, the evidence presently available indicates that it is more appropriate to use ecotypes rather than such subspecies designations.

Finally, I wish to reemphasise the importance of interfertility in species definition. At present, there is no evidence that the so called 'new' species of *Kandelia*, *K. obovata*, is genetically isolated from or reproductively incompatible with the long established, polytypic species of *Kandelia candel*. Long may *K. candel* endure!

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