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THE WORKING PARTY ON CHEMICALS, PESTICIDES AND BIOTECHNOLOGY**

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Series on Harmonisation of Regulatory Oversight in Biotechnology No.36

**CONSENSUS DOCUMENT ON THE BIOLOGY OF THE CAPSICUM ANNUUM COMPLEX (CHILI
PEPPERS, HOT PEPPERS AND SWEET PEPPERS)**

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OECD Environment, Health and Safety Publications

Series on Harmonisation of Regulatory Oversight in Biotechnology

No. 36

**Consensus Document on the Biology
of the *Capsicum annuum* Complex
(Chili peppers, Hot peppers and Sweet peppers)**

Environment Directorate

Organisation for Economic Co-operation and Development

Paris 2006

ABOUT THE OECD

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FOREWORD

Consensus documents contain information for use during the regulatory assessment of a particular product. In the area of crop biosafety, these are being published on information on the biology of certain crop species, selected traits that may be introduced into crop species, and biosafety issues arising from certain general types of modifications made to crops.

This document addresses the biology of the *Capsicum annuum* complex (Chili peppers, Hot peppers and Sweet peppers). Korea served as the lead country in the preparation of this document in collaboration with Mexico and the United States.¹ The draft has been revised on a number of occasions based on the inputs from other member countries. At the 17th meeting of the Working Group (24-26 October, 2005), it was agreed that the document be forwarded to the joint Meeting of OECD's Chemicals Committee and Working Party on Chemicals, Pesticides and Biotechnology, which then agreed that this document be declassified.

¹ The institutes that participated in the preparation of the draft of this document are: The National Institute of Agricultural Biotechnology, Young-Yang Chili Pepper Experimental Station, and National Horticultural Research Institute in Korea; Animal and Plant Health Inspection Service, and Chili Pepper Institute of New Mexico State University in the United States; and CIBIOGEM in Mexico.

TABLE OF CONTENTS

PREAMBLE.....	11
SECTION I. INTRODUCTION.....	13
SECTION II. TAXONOMY AND CYTOLOGY.....	14
SECTION III. CENTRES OF ORIGIN AND DISTRIBUTION.....	16
SECTION IV. MORPHOLOGICAL CHARACTERS AND MOLECULAR MARKERS	19
A. Morphological characters for identification.....	19
B. Molecular markers.....	19
SECTION V. REPRODUCTIVE BIOLOGY AND ECOLOGY	21
A. Reproductive organs (morphology, development), fertilisation, dispersal and germination	21
A.1. Flower.....	21
A.2. Pollen and fertilisation.....	21
A.3. Fruit	22
A.4. Fruit dispersal	23
A.5. Seed and germination	23
B. Sexual reproduction.....	24
B.1. Pollination.....	24
B.2. Crossability and hybridisation	24
C. Asexual reproduction	25
SECTION VI. CROP PRODUCTION AND USE.....	26
A. Environmental conditions	26
B. Agricultural practices	26
C. Biotic stresses.....	27
D. Experience and world statistics.....	28
SECTION VII. MODERN BIOTECHNOLOGY	29
SECTION VIII. REFERENCES	30
QUESTIONNAIRE TO RETURN TO THE OECD.....	47

Tables

Table 1. Classification of <i>Capsicum annuum</i>	14
Table 2. The species of <i>Capsicum</i> and their known or apparently natural distributions	18
Table 3. Morphological characters that generally differentiate the domesticated species of <i>Capsicum</i> ..	19
Table 4. Crossability of <i>Capsicum annuum</i> with other <i>Capsicum</i> in the three complexes of domesticated species.....	25

PREAMBLE

Genetically engineered crops (also known as transgenic crops) such as maize, soybean, rapeseed and cotton have been approved for commercial use in an increasing number of countries. During the period from 1996 to 2005, for example, there was more than fifty-fold increase in the area grown with transgenic crops worldwide, reaching 90 million hectares in 2005.² Such approvals usually follow a science-based risk/safety assessment.

The environmental safety/risks of transgenic organisms are normally based on the information on the characteristics of the host organism, the introduced traits, the environment into which the organism is introduced, the interaction between these, and the intended application. The OECD's Working Group on Harmonisation of Regulatory Oversight in Biotechnology decided at its first session, in June 1995, to focus its work on identifying parts of this information, which could be commonly used in countries for environmental safety/risk assessment to encourage information sharing and prevent duplication of effort among countries. Biosafety Consensus Documents are one of the major outputs of its work.

Biosafety Consensus Documents are intended to be a "snapshot" of current information on a specific host organism or trait, for use during regulatory assessments. They are not intended to be a comprehensive source of information on everything that is known about a specific host or trait; but they do address the key or core set of issues that member countries believe are relevant to risk/safety assessment. This information is said to be mutually acceptable among member countries. To date, 24 Biosafety Consensus Documents have been published. They include documents which address the biology of crops, trees and micro-organisms as well as those which address specific traits which are used in transgenic crops.

In reading the Consensus Documents, it is useful to consult two additional texts. The first, entitled *An Introduction to the Biosafety Consensus Documents of OECD's Working Group for Harmonisation in Biotechnology* explains the purpose of the Consensus Documents and how they are relevant to risk/safety assessment. It also describes the process by which the documents are drafted using a "lead country" approach. The second text is *Points to Consider for Consensus Documents on the Biology of Cultivated Plants*. This is a structured checklist of "points to consider" for authors when drafting or for those evaluating a Consensus Document. Amongst other things, this text describes how each point is relevant to risk/safety assessment.

The Consensus Documents are of value to applicants for commercial uses of transgenic organisms, regulators in national authorities as well as the wider scientific community. As each of the documents may be updated in the future as new knowledge becomes available, users of Consensus Documents are encouraged to provide any information or opinions regarding the contents of this document or indeed, OECD's other harmonisation activities. If needed, a short pre-addressed **questionnaire** is attached at the end of this document that can be used to provide such comments.

² Clive James (2005), International Service for the Acquisition of Agri-biotech Applications (<http://www.isaaa.org/>)

ENV/JM/MONO(2006)2

The published Consensus Documents are also available individually from OECD's website (<http://www.oecd.org/biotrack>) at no cost.

SECTION I. INTRODUCTION

1. *Capsicum annuum* L. is a dicotyledonous flowering plant commonly grown worldwide, with many general names in English, such as hot pepper, chili, chilli or chile pepper, and as well sweet pepper and bell pepper. Sometimes the plant is just called pepper, which however is often reserved for the earlier known Asian *Piper nigrum* (black pepper, white pepper) in the family Piperaceae. The pre-Columbian, indigenous Nahua (Aztec) Amerindian name for the plant was transcribed as chilli or chili, and the usual name in Spanish is chile, which results in the plurals of chillies, chilies, and chiles (Bosland, 1996). Other broad names for *C. annuum* relate more to particular varieties or strains, culinary uses, and ripeness, such as jalapeño, Cayenne, pimento (pimiento), paprika, red, and green peppers. Furthermore, four other less commonly cultivated *Capsicum* species are also considered chile peppers, and two of these species are similar and closely related to *C. annuum*.

2. *Capsicum annuum* is usually grown as a herbaceous annual in temperate areas. However, ecologically it is a perennial shrub in tropical areas (which may live a few years to a few decades), and it can be grown as a perennial in climate-controlled greenhouses. This species includes the vast majority of the cultivated pungent and non-pungent (sweet) *Capsicum* peppers in temperate as well as some tropical areas. In the species *C. annuum* throughout the world, there is phenotypic diversity in plant habit and especially in shapes, sizes, colours, pungency, and other qualities of the fruits (Andrews, 1995, 1998, 1999; DeWitt and Bosland, 1996; Greenleaf, 1986). This immense horticultural, agricultural and biological diversity has helped to make *C. annuum* globally important as a fresh and cooked vegetable (*e.g.* for salads, warm dishes, pickled) and a source of food ingredients for sauces and powders and as a colourant, which is used as well in cosmetics (Andrews, 1995, 1999; Bosland, 1994; Bosland and Votava, 2000). Moreover, the species is used medicinally and medically, and provides the ingredient for a non-lethal deterrent or repellent to some human and animal behaviours (Krishna De, 2003; Cordell and Araujo, 1993; Palevitch and Craker, 1995; Cronin, 2002; Cichewicz and Thorpe, 1996; Reilly *et al.*, 2001). Chili peppers are also cultivated ornamentally especially for their brightly glossy fruits with a wide range of colours.

3. Chili pepper comprises numerous chemicals including steam-volatile oil, fatty oils, capsaicinoids, carotenoids, vitamins, protein, fibre, and mineral elements (Bosland and Votava, 2000; Krishna De, 2003). Many chili pepper constituents have importance for nutritional value, flavour, aroma, texture, and colour. The ripe fruits are especially rich in vitamin C (Osuna-García *et al.*, 1998; Marin *et al.*, 2004). The two chemical groups of greatest interest are the capsaicinoids and the carotenoids. The capsaicinoids are alkaloids that give hot chili peppers their characteristic pungency. The rich supply of carotenoids contributes to chili peppers' nutritional value and colour (Britton and Hornero-Méndez, 1997; Hornero-Méndez *et al.*, 2002; Pérez-Gálvez *et al.*, 2003).

SECTION II. TAXONOMY AND CYTOLOGY

4. The genus *Capsicum* L. is in the large family Solanaceae, which includes as food the potato (*Solanum tuberosum*), tomato (*Lycopersicon esculentum* or *Solanum lycopersicum*), tree tomato (*Cyphomandra betacea* or *Solanum betaceum*), eggplant (*Solanum melongena*), African eggplants (*Solanum macrocarpon*, *S. aethiopicum*), husk or strawberry tomato (*Physalis pruinosa*) and Cape gooseberry (*P. peruviana*), as well as tobacco (*Nicotiana tabacum*), medicinal plants such as deadly nightshade (*Atropa belladonna*) and *Datura stramonium*, ornamentals such as tree daturas (*Brugmansia*) (which are also hallucinogenic) and *Petunia*, and weeds such as black nightshade (*Solanum nigrum*) (Knapp, 2002; Hunziker, 2001; George, 1985). *Capsicum* is in the subfamily Solanoideae and tribe Capsiceae (Olmstead *et al.*, 1999; Knapp, 2002; Knapp *et al.*, 2004; Hunziker, 2001). The genus *Capsicum* consists of about 25 wild and 5 domesticated species (Table 2) (IBPGR, 1983; Eshbaugh, 1993; Bosland and Votava, 2000).

5. The five variously domesticated species are *Capsicum annuum* (Table 1), *C. frutescens*, *C. chinense*, *C. baccatum* and *C. pubescens* (Heiser and Smith, 1953; Smith and Heiser, 1957; Heiser, 1985). *Capsicum annuum*, *C. frutescens* and *C. chinense* are grouped in a taxonomic complex which has conventionally three, or perhaps two or one species (Pickersgill, 1988), with the three clusters of domesticated plants appearing to be more divergent than their wild progenitors (Heiser, 1985; Eshbaugh, 1993; Prince *et al.*, 1995; Idu and Ogbe, 1997; Park *et al.*, 1999; Bosland and Votava, 2000; Walsh and Hoot, 2001; Jarret and Dang, 2004; Ryzhova and Kochieva, 2004; Baral and Bosland, 2004). The remaining two domesticated species are in other taxonomic complexes of the genus (Eshbaugh, 1993; Tong and Bosland, 1999; Walsh and Hoot, 2001). Both are little used beyond Latin America, although *C. baccatum* var. *pendulum* (Willd.) Eshbaugh, the variety that has been extensively domesticated, is much used there. For a while, the name *C. frutescens* instead of *C. annuum* was applied to the domesticated chili peppers (Bailey, 1923), so in some literature caution is needed to ascertain whether the plants discussed are actually *C. annuum* (which is more likely), or *C. frutescens* itself (*sensu stricto*, *i.e.* in the narrowly circumscribed sense) or perhaps another of these species (Heiser and Pickersgill, 1969; Heiser, 1985).

Table 1. Classification of *Capsicum annuum*

Taxonomic placement	Scientific name
Kingdom	Plantae
Division	Magnoliophyta
Class	Magnoliopsida
Order	Solanales
Family	Solanaceae
Genus	<i>Capsicum</i>
Species	<i>annuum</i>
Botanical varieties	var. <i>glabriusculum</i> (synonym var. <i>aviculare</i>) var. <i>annuum</i>

6. *Capsicum* species are diploids, with most having 24 chromosomes ($n = x = 12$), but with several wild species having 26 chromosomes ($n = x = 13$) (Table 2) (Pickersgill, 1991; Tong and Bosland, 2003). *Capsicum annuum* has 24 chromosomes; usually 2 pairs (or sometimes 1) are acrocentric, and 10 (or 11)

pairs metacentric or sub-metacentric (Lanteri and Pickersgill, 1993). Its nuclear DNA content (determined by flow cytometry and Feulgen densitometry) has been reported to have a mean 1C-value of 3.38 picograms per nucleus, which Moscone *et al.* (2003) discuss in relation to other reports with varying methodology that range from 2.76 to 5.07 pg per nucleus. The total length of the chili pepper genome has been estimated to be between 1498 cM and 2268 cM, which is approximately two to three times larger than the tomato genome (Kang *et al.*, 2001; Schreiber, 2004).

SECTION III. CENTRES OF ORIGIN AND DISTRIBUTION

7. The centre of diversity for *Capsicum* is in south-central South America (Eshbaugh, 1980; Hunziker, 1979; D'Arcy and Eshbaugh, 1974; Gonzalez and Bosland, 1991; WWF and IUCN, 1997), with the majority of species having some range in Brazil and/or Bolivia. Some of the non-domesticated species are gathered for occasional use. The primary centre of origin for domesticated *C. annuum* is in semi-tropical Mexico (Hernández-Verdugo *et al.*, 1999, 2001a; Andrews, 1995; Long-Solís, 1998; Whitmore and Turner, 2002). The four other domesticated species are usually believed to have originated in South America (Eshbaugh *et al.*, 1983; Walsh and Hoot, 2001; Denevan, 2001). The centres of origin and domestication of the other two species in the *C. annuum* complex are not as clear (*cf.* Clement, 1999). Amazonia (in the northern area) is considered the centre for *C. chinense* ("habanero") (Velez, 1991; Toquica *et al.*, 2003), and western Amazonia is perhaps the centre for *C. frutescens* ("tabasco"), which is more domesticatedly variable in Central America (Heiser, 1985; Hernández-Verdugo *et al.*, 1999). Bolivia is considered the centre of domestication for *C. baccatum* (ají) (in the subtropical east) and *C. pubescens* (rocoto) (in the mid-elevation Andes, where known only in cultivation) (Eshbaugh *et al.*, 1983; Eshbaugh, 1993).

8. By molecular analysis, Loaiza-Figueroa *et al.* (1989) confirmed that the centre of domestication of *C. annuum* var. *annuum*, the cultivated variety, is the upland region (Sierra Madre Oriental) of central-eastern Mexico (in the states of Nuevo León, Tamaulipas, San Luis Potosí, Veracruz and Hidalgo). Its ancestor probably is the wild chiltepín (bird pepper), *C. annuum* var. *glabriusculum* (Dunal) Heiser & Pickersgill, which has a range of unclear natural extent from southern USA through Mesoamerica to Colombia and the Caribbean, and is sometimes wild-harvested still and semi-domesticated as well (Eshbaugh, 1993; Hernández-Verdugo *et al.*, 2001a; Votava *et al.*, 2002; Vásquez-Dávila, 1996; Guzmán *et al.*, 2005).

9. The earliest archaeological evidence of *Capsicum* being used dates to 10,500 BP (*C. baccatum*) and 10,000-9,500 BP (*C. chinense*) in the western Central Andes of Peru (Brack, 2003; Smith, 1980). Substantial evidence in Peruvian dry coastal river valleys, with specimens increasing from rare to moderately abundant through eight millennia, indicates expanding cultivation and domestication of *Capsicum* (Pearsall, 2003). *Capsicum frutescens* is recognised in the northwestern area by 4400-3200 BP (Brack, 2003). Intriguingly, *Capsicum* seems to be absent from the more recent Chiribaya culture of 1100-600 BP in far southern Peru (Flamini *et al.*, 2003), even though earlier (2200-1400 BP) in southwestern Peru *C. frutescens* was being used. The importance of *Capsicum* is suggested by an obelisk from Chavín de Huántar (~ 2800 BP) in the north-central Peruvian Andes, featuring a foundational Earth-crocodilian associated with (apparently) gourd, chili pepper, manioc (cassava) and peanut (Brotherston, 1979; Miller and Burger, 1995). Similarly, there is archaeological evidence from about 9000 BP for the use and subsequent domestication of *Capsicum annuum* in central-eastern and south-central Mexico in the states of Tamaulipas (near Ocampo), Puebla (Tehuacán Valley) and Oaxaca (Guilá Naquitz) (Pickersgill, 1984; Bosland, 1996; *cf.* Smith, 2001, 2005).

10. *Capsicum* was brought to Europe by Columbus in 1493 as the peppery spice that signified the success of his quest, and the early European voyagers to the Caribbean, Mesoamerica and South America encountered a plethora of variety and landraces of this common food as well as medicinal plant (Sauer, 1966; Long-Solís, 1998). The ready appeal of *Capsicum* was such that within half a century it had been distributed as far as Asia, and it has been integrated and continues to be diversified in cultures worldwide

as it had been originally in the Americas (Ferrão, 1992; Andrews, 1992, 1995, 1998, 1999; DeWitt and Bosland, 1996; Eshbaugh, 1983; Yamamoto and Nawata, 2004, 2005).

11. The species of *Capsicum* were listed with their seemingly natural distributions by the International Board for Plant Genetic Resources (IBPGR, 1983) and updated by Eshbaugh (1993), Hernández-Verdugo *et al.* (1999) and Bosland and Votava (2000); they are listed in Table 2 as currently understood. There is modest uncertainty on the generic limits of *Capsicum* and more uncertainty on its tribal relatives (which at minimum include *Lycianthes*) (Eshbaugh, 1993; Hunziker, 2001; Knapp, 2002), and a lack of consensus on the number and in a few cases the botanical names of the known *Capsicum* species, and on the truly natural distributions of several species (rather than confounding naturalised with native populations).

Table 2. The species of *Capsicum* and their known or apparently natural distributions; those with haploid chromosome number $n = 13$ rather than $n = 12$ are noted (Tong and Bosland, 2003). The five domesticated species are grouped into the *C. annuum* complex (3 spp.) (C_A), the *C. baccatum* complex (C_B), and the *C. pubescens* complex (C_P)

Species	Known or probable natural distribution
<i>C. annuum</i> L. (C_A)	southern USA to Colombia
<i>C. baccatum</i> L. (C_B)	Peru, Bolivia, Paraguay, Argentina and Brazil
<i>C. buforum</i> Hunz.	southern Brazil
<i>C. campylopodium</i> Sendtner; $n = 13$	southern Brazil
<i>C. cardenasii</i> Heiser & P.G. Smith (C_P)	northeastern Bolivia
<i>C. chacoense</i> Hunz. (C_B or C_A)	Argentina, Paraguay and Bolivia
<i>C. chinense</i> Jacq. (C_A)	(northern) Amazonian South America
<i>C. coccineum</i> (Rusby) Hunz.	Bolivia and Peru
<i>C. cornutum</i> (Hiern) Hunz.	southern Brazil
<i>C. dimorphum</i> (Miers) Kuntze	Colombia
<i>C. dusenii</i> Bitter	southeastern Brazil
<i>C. eximium</i> Hunz. (C_P)	Bolivia and northern Argentina
<i>C. flexuosum</i> Sendtner	Argentina, Brazil and Paraguay
<i>C. frutescens</i> L. (C_A)	western Amazon (Colombia to Peru)
<i>C. galapagoense</i> Hunz. (C_A)	Galápagos Islands (Ecuador)
<i>C. geminifolium</i> (Dammer) Hunz.	Colombia and Ecuador
<i>C. hookerianum</i> (Miers) Kuntze	Ecuador and northwestern Peru
<i>C. lanceolatum</i> (Greenman) Morton & Standley; $n = 13$	Honduras, Guatemala and Mexico
<i>C. leptopodium</i> (Dunal) Kuntze	Brazil
<i>C. minutiflorum</i> (Rusby) Hunz.	Argentina, Paraguay and Bolivia
<i>C. mirabile</i> Mart. ex Sendtner; $n = 13$	southern Brazil
<i>C. parvifolium</i> Sendtner	northeastern Brazil, Venezuela and Colombia
<i>C. praetermissum</i> Heiser & P.G. Smith (C_B) [synonym <i>C. baccatum</i> var. <i>praetermissum</i> (Heiser & P.G. Smith) Hunz.]	southern Brazil
<i>C. pubescens</i> Ruiz & Pavón (C_P)	Bolivia to Colombia [only in cultivation]
<i>C. rhomboideum</i> (Dunal) Kuntze [synonym <i>C. ciliatum</i> (Kunth) Kuntze]; $n = 13$	Mexico to Peru
<i>C. schottianum</i> Sendtner; $n = 13$	southern Brazil, Paraguay and Argentina
<i>C. scolnikianum</i> Hunz.	northwestern Peru
<i>C. tovarii</i> Eshbaugh, P.G. Smith & Nickrent (C_B)	south-central Peru
<i>C. villosum</i> Sendtner	southern Brazil

Source: Tong and Bosland, 1999; Walsh and Hoot, 2001; Jarret and Dang, 2004; Ryzhova and Kochieva, 2004

SECTION IV. MORPHOLOGICAL CHARACTERS AND MOLECULAR MARKERS

A. Morphological characters for identification

12. The five domesticated species are differentiated by using morphological characters that rely primarily on colour and morphology of flowers and seeds (Andrews, 1995; DeWitt and Bosland, 1996), as shown in Table 3. However, identifying some plants in the diverse *C. annuum* complex can be problematic (Pickersgill *et al.*, 1979; Bosland and Votava, 2000; Jarret and Dang, 2004; Baral and Bosland, 2004). Capsaicinoid profiles are not reliable as unique indicators for identification, though the profile may be useful as a supplementary character. In one study (7-58 accessions per species), the accuracy of identification based solely on capsaicinoid profiles, in the *C. annuum* complex was 82% of the *C. chinense* accessions, 57% for *C. annuum* and just 20% for *C. frutescens* (but its sample was only 10 accessions); and similarly was 59% for *C. baccatum*, and 86% for the distinctive *C. pubescens* (Zewdie and Bosland, 2001).

Table 3. Morphological characters that generally differentiate the domesticated species of *Capsicum*

Species	Flowers per node	Calyx	Corolla colour	Corolla-lobe basal spots	Anther colour	Seed colour
<i>C. annuum</i> var. <i>annuum</i>	1 (-5)	no ring; often teeth	white to dingy white (rarely purple)	none	blue-purple	straw (tan)
<i>C. frutescens</i>	usually 2-4 (1-6)	no ring; usually no teeth	greenish white or greenish	none	blue-purple	straw (tan)
<i>C. chinense</i>	(1-) 2 (-5)	annular ring; no teeth	greenish white or white	none	blue	straw (tan)
<i>C. baccatum</i> var. <i>pendulum</i>	1 (-2)	no ring; teeth	white (cream) or greenish-white	yellow-green	white to yellowish	straw (tan)
<i>C. pubescens</i>	1	no ring; teeth	purple or purple-white	none	purple (purple- white)	black (brown/ black)

Source: after Lippert *et al.*, 1966; Heiser, 1985; Greenleaf, 1986; Eshbaugh, 1993; Jarret and Dang, 2004

13. Cultivated *Capsicum annuum* var. *annuum* is very diverse regionally and worldwide (*e.g.* DeWitt and Bosland, 1996; Andrews, 1995, 1998), having a wealth of innumerable strains, landraces and varieties that defy both facile description (IPGRI *et al.*, 1995; Zewdie *et al.*, 2004) and clustering into an inclusive and practicable classification (Bosland and Votava, 2000). Sometimes typical characteristics (fruit shape, size, and pungency) have been featured and organised, recognising the Cerasiforme Group (cherry peppers), Conoides Group (conical peppers), Longum Group (*e.g.* Cayenne peppers) and Grossum Group (blocky sweet or bell peppers) (*cf.* Mabblerley, 1998; Bailey, 1923), but as more plants are considered the array of variations and combinations of notable traits increases (*e.g.* fruit sizes and shapes intermediate, whether fruits are erect or pendent), and the groups become less distinct and meaningful.

B. Molecular markers

14. Various molecular markers have been used for identification of chili peppers, and to evaluate their germplasm diversity. A review is provided by Lefebvre (2005). Rodriguez *et al.* (1999) found diagnostic RAPD (randomly amplified polymorphic DNA) markers for four of the domesticated species

(and *C. chacoense*), but not for *C. frutescens*. Use of isozymes has focused predominantly on measuring genetic variability, and clarifying phylogenetic relationships within the genus (Eshbaugh, 1993). Conicella *et al.* (1990) analysed esterase isozymes in 15 accessions of *C. annuum* from the Americas; these data plus cytological data also provided evidence that Mexico is the centre of domestication for *C. annuum*.

15. Prince *et al.* (1995) utilised RAPDs in studying molecular polymorphism in *C. annuum*. Lefebvre *et al.* (2002) developed an integrated intraspecific *C. annuum* molecular linkage map using phenotypic and isozyme markers, known functional genes, RAPDs, RFLPs (restriction fragment length polymorphisms) and AFLPs (amplified fragment length polymorphisms) from F₁ and F₂ hybrids derived from double-haploid *C. annuum* populations. Using RAPDs and AFLPs on a broad array of *C. annuum* types (from 34 accessions of nine countries), Paran *et al.* (1998) separated large-fruited sweet peppers from small-fruited pungent peppers, and found more genetic variation among the pungent cultivars. Tam *et al.* (2005) found the SSAP (sequence-specific amplification polymorphism) marker system generally more informative than using AFLPs or SSRs (simple sequence repeats or microsatellites). They had similar overall results between large-fruited sweet (bell) types and conical types, but within their pungent as well as sweet conical types the grouping of some cultivars shifted depending on which of the three marker systems was employed.

16. Tanksley (1984b) developed the first linkage map of *Capsicum* by studying segregating isozymes in an interspecific cross between *C. annuum* and *C. chinense*. Genomic similarities and differences between *Capsicum* and *Lycopersicon* were studied by Tanksley *et al.* (1988) to construct the first RFLP linkage map of chili pepper (with 85 loci). A more complete map was developed by Prince *et al.* (1993), and Livingstone *et al.* (1999) provided a still more comprehensive comparative map with over 1000 loci using mainly AFLP and RFLP markers. Repetitive DNA sequences make up a maximum of 10% of the chili pepper genome, which overall is at least four times more copies than in tomato (Schreiber, 2004). Kang *et al.* (2001) constructed a more complete interspecific (*C. annuum* × *C. chinense*) F₂ molecular linkage map using mainly pepper-derived RFLP probes and AFLP markers, and Lee *et al.* (2004a) augmented the map using SSRs. Paran *et al.* (2004) constructed an integrated genetic linkage map of these *Capsicum* spp., consisting of 2262 diverse markers (including several known gene sequences) and covering 1832 cM and 13 linkage groups (with only 15 gaps > 10 cM remaining). An RFLP-based map (92 markers) of an interspecific (*C. annuum* × *C. frutescens*) BC₂ population has also been constructed (Rao *et al.*, 2003).

SECTION V. REPRODUCTIVE BIOLOGY AND ECOLOGY

A. Reproductive organs (morphology, development), fertilisation, dispersal and germination

A.1. Flower

17. *Capsicum annuum* starts flowering at the axil of the first branching node, with subsequent flowers forming at each additional node (Bosland and Votava, 2000). Usually *C. annuum* has a solitary flower at the axil (Bosland and Gonzalez, 1994), although some accessions have a few clustered flowers between which there are short internodes (Smith and Heiser, 1951) (Table 3). Flower differentiation is not affected by daylength (Cochran, 1942). The most important factor determining differentiation is air temperature, especially at night (Bosland and Votava, 2000; Aloni *et al.*, 1999; Rylski, 1972).

18. The *Capsicum* flower is bisexual, hypogynous and usually pentamerous (Bosland and Votava, 2000). The flowers are complete, with calyx, corolla, and male and female sex organs. The diameter of a *C. annuum* flower is 9-15 mm. The *Capsicum* calyx is broadly campanulate, ribbed, about 2 mm long, and truncate or undulate to weakly or prominently dentate with 5-7 teeth. The short-tubed corolla is rotate in most *Capsicum* species, with usually 5 but sometimes 6-7 (-8) petals in some species. The number of corolla lobes and stamens is equal. Typically the flowers have 5 stamens; the filaments are white or violet depending on the species (or variety), with the usually connivent to free anthers varying from bluish-purple to yellow and white depending on the species (*e.g.* Table 3) (Dharamadhaj and Prakash, 1978). The pistil comprises an ovary of 2-3 (-4) carpels that is 2-5 mm long and 1.5-5 mm in diameter, a style 3.5-6.5 mm long, and a capitate papillate stigma slightly wider than the style. The style extends well beyond to just beyond the anthers or may be even with them, or it may be slightly exceeded by the anthers.

19. The daily start of anthesis apparently is controlled by daylength (Aleemullah *et al.*, 2000). The corolla typically opens within the first 3 hours after sunrise, and the petals remain open for less than a day; there also can be a smaller peak of anthesis in the afternoon. Hirose (1957) found dehiscence of the anthers to occur late in the morning, between 10 am and noon. The anthers open lengthwise from typically 1 hr after the flower opens to even 10 hrs afterward, but they frequently fail to dehisce entirely, or may dehisce the next morning if the flower opens in late afternoon (Aleemullah *et al.*, 2000; *cf.* Horner and Wagner, 1992). Depending on the environmental conditions and variety, the period of receptivity of the stigma is 5-8 days, from several days before anthesis to fewer days afterwards, with maximum fertility on the day of anthesis (Cochran and Dempsey, 1966; Barai and Roy, 1986; Aleemullah *et al.*, 2000).

A.2. Pollen and fertilisation

20. The pollen grains of chili pepper are medium to light yellow, subspheroidal, pitted, and tricolporate with longitudinal grooves (Bosland and Votava, 2000). The plant has about 1-1.5 mg of pollen per flower (Quagliotti, 1979), with 11,000-18,000 pollen grains in a single anther (Hirose, 1957). Air temperature has a large effect on pollen formation and viability. Temperatures above 30°C occurring 15 days prior to anthesis cause pollen sterility (Cochran, 1938), and night temperatures of 10 ± 2 °C reduce the number and germinability of pollen grains (Shaked *et al.*, 2004). The optimal temperature for pollen germination is 20-25°C. Pollen tube growth from the stigma to the egg has been reported to take 6 to 42 hrs. In detailed anatomical studies, Cochran (1938) found that fertilisation occurred 42 hrs after pollination

in plants grown at 27°/21°C, whereas Kato (1989) found that 36 hrs were needed for the fertilisation process.

21. Male sterility is found in *Capsicum*, controlled by cytoplasmic and nuclear genes (Shifriss, 1997; Wang *et al.*, 2004; Kalloo *et al.*, 2002). In plants of both types, the anthers may be small and shrunken and blue-violet, with little or no viable pollen (Wien, 1997), or there may be no anthers (Derera *et al.*, 2005).

A.3. Fruit

22. There is extensive diversity in fruit shape, size, wall thickness and fleshiness, colour and pungency (Andrews, 1995; IPGRI *et al.*, 1995), determined by genetic and environmental factors. Among the innumerable varieties of *C. annuum*, the diversification of shapes of the pod (fruit) is striking — *e.g.* blocky (or lantern- or bell-shaped), globose, oblong (sausage-shaped), ovoid, conical, cylindrical, banana-like (curved); and smooth, grooved, lumpy or wrinkled. The length of the pod varies from less than 1 to 32.5 cm. The pedicel length also varies in different pod types (over several cm), and the fruit may be erect to pendent (deflexed). Fruit colours range from green, yellow, orange and red to purple, brown, black, and white as well. Some of the genetics of fruit colour and shape are becoming well understood (Ben Chaim *et al.*, 2003; Thorup *et al.*, 2000; Huh *et al.*, 2001).

23. Morphologically the *Capsicum* fruit is a berry, sometimes with a few stone cells (sclerified inclusions in the fleshy portion) (Knapp, 2002). The pericarp consists of epidermal cells in regular order with a thick-grooved cuticle. Several rows of collenchymatously thickened beaded cells constitute the hypodermis. The mesocarp is formed by thick-walled beaded cells; the inner mesophyll cells are thin-walled ground parenchyma and fibrovascular bundles. Giant cells (perhaps unique to *Capsicum*) occur on the inner wall of the endocarp (Fridvalsky and Nagy, 1966). The vascular bundles consist of xylem tissue with spiral vessels and phloem tissue. The pod has two, three or four locules, with each corresponding wall of the axile placenta having vesicles for production of capsaicinoids (Suzuki *et al.*, 1980).

24. Usually there are many more flowers than fruits (Marcelis *et al.*, 2004). The most obvious sign of assimilate competition or dominance among the organs is abscission of flowers and small fruits during the most active fruit-growth period, resulting in a cycling of flowering and fruit set (Hall, 1977; Clapham and Marsh, 1987; Bhatt and Srinivasa Rao, 1997; Marcelis *et al.*, 2004). The most actively growing organ of a chili pepper plant after flowering is the fruit (Hall, 1977; Beese *et al.*, 1982; Marcelis and Baan Hofman-Eijer, 1995). Fruit growth is dependent on ovule growth (whether fertilised). The fruit is ordinarily seeded, but parthenocarpic forms exist (Heuvelink and Körner, 2001). The seed set affects development and subsequent growth of the fruit; on average there is a direct linear relationship between the number of seeds per fruit and final fruit size, until saturation at perhaps over 200 seeds per fruit (Marcelis and Baan Hofman-Eijer, 1997). The number of seeds per fruit ranged from 1 to 34 in wild northwestern Mexico populations of *C. annuum* (Hernández-Verdugo *et al.*, 2001b). A low of 50-100 seeds per cultivated fruit (20-30% of maximum) is sufficient for maximal fruit set (Marcelis and Baan Hofman-Eijer, 1997); blocky sweet pepper (bell pepper) may average 150-300 seeds per fruit (Aloni *et al.*, 1999).

25. The time from anthesis to a fully grown fruit varies considerably among different pod types (Bosland and Votava, 2000). Typically cultivated fruit reaches the mature green stage in 35-50 days after the flower is pollinated. This stage is horticulturally ripe for some uses, but still physiologically immature. Fruit maturity depends on the cultivar and the environmental conditions before and during maturation (Perry *et al.*, 1993; Montes Hernández *et al.*, 2004). The fruits are characterised as non-climacteric in ripening (Lownds *et al.*, 1993), apparently lacking the typical increase in CO₂ and ethylene production as they ripen (Saltveit, 1977).

26. The fruits of most *Capsicum* are pungent, because the placenta accumulates capsaicinoids (e.g. capsaicin) (Zewdie and Bosland, 2001; Thompson *et al.*, 2005), except in domesticated non-pungent (sweet) varieties which are mostly developed in *C. annuum* (Bosland and Votava, 2000). The pungency trait is controlled at a single locus on chromosome 2; when the pungency gene *Pun1* (also called *C*) is homozygous recessive (i.e. present as *pun1/pun1* or *cc*), the capacity to make capsaicinoids is lost (Stewart *et al.*, 2005; Blum *et al.*, 2002). In the pungent chili peppers, other genes variously affect the synthesis of capsaicinoids (Blum *et al.*, 2003), and production is also affected by physiological interactions and the environment (Zewdie and Bosland, 2000a; Estrada *et al.*, 2002; Sung *et al.*, 2005). The individual fruit's pungency (content of capsaicinoids) is affected by its node position on the plant, whereas its capsaicinoid profile remains fairly constant (Zewdie and Bosland, 2000b; Estrada *et al.*, 2002; Kirschbaum-Titze *et al.*, 2002). Capsaicinoids increase with fruit growth to a maximum (e.g. 40-50 days after fruit set), then decline (Contreras-Padilla and Yahia, 1998). Capsaicinoids can be transported within the plant, with different capsaicinoid profiles found in stems and leaves (Estrada *et al.*, 2002).

A.4. Fruit dispersal

27. The red fruits of wild *C. annuum* var. *glabriusculum* attract birds, which eat them and disperse viable seeds, but their pungency discourages consumption by wild mammals (Vásquez-Dávila, 1996; Tewksbury *et al.*, 1999; Tewksbury and Nabhan, 2001). Rats experimentally fed hot chili peppers for 2-11 months became desensitised to aversion, but indifferent rather than developing a preference for this spicy food (Rozin *et al.*, 1979). Nonetheless, the widespread and common little yellow-shouldered bat (*Sturnira lilium*), which sometimes favours solanaceous fruits (Passos *et al.*, 2003; Galindo-González *et al.*, 2000), has been reported to consume pungent *Capsicum* in northwestern Argentina and disperse the seeds — which is favoured by local people who recognise this increases the number of wild plants, as they gather the fruits for home seasoning and village marketing (Iudica, 1999).

A.5. Seed and germination

28. The seed develops from a campylotropous ovule (Dharamadhaj and Prakash, 1978). Within a pod, the many seeds are attached to the placenta walls in close rows, mainly near the calyx end. The seeds are disk-like with a deep chalazal depression. The embryo is surrounded by a well-defined endosperm which makes up the bulk of food reserves for the embryo and young seedling. The endosperm lies directly in front of the radicle and consists of seven to nine thick cells (Watkins *et al.*, 1985). *Capsicum annuum* seeds have mainly protein and lipids as storage reserves (Chen and Lott, 1992). The seed is covered by a parchment-like seed coat, which does not cause a mechanical restriction to germination (Watkins and Cantliffe, 1983b). Seed colour inheritance involves at minimum about three genes (Zewdie and Bosland, 2003). Seed size is somewhat dependent on the variety and growing conditions. Seed mass maturity may occur about 50 days after anthesis, with 10-12 more days required for maximum potential longevity but 17-21 days for maximal seedling dry weight (based on variation in time from sowing to emergence) (Demir and Ellis, 1992). An average *C. annuum* seed is about 5.3 mm long, 4.3 mm wide and 1 mm thick, with a surface area of 33 mm² (Chen and Lott, 1992).

29. Freshly harvested seeds of certain wild *Capsicum* species can exhibit dormancy (Bosland and Votava, 2000; Wien, 1997; IBPGR, 1983). An after-ripening period at room temperature may be required to remove dormancy (Randle and Homna, 1981). As *C. annuum* seeds age and lose viability (Ozcoban and Demir, 2002) they may become brown. Seed dormancy may be broken by treatment with 0.2 M KNO₃ under white light (750-1250 lux) and alternating temperatures (30°/20°C or 30°/15°C) (cf. Hernández-Verdugo *et al.*, 2001b). Seeds of cultivated *C. annuum* can be cryopreserved at -196°C and moisture content of 4.7-11.5%, and subjected to rapid or slow freezing and thawing (Quagliotti and Comino, 2003).

30. *Capsicum* species seeds germinate well in a constant temperature range between 15°C and 30°C (Randle and Homna, 1980; *cf.* Dell'Aquila, 2004), and do not germinate when exposed to temperatures below 8°C or above 40°C (Choi, 1985). No special light requirements are necessary for germination of domesticated chili pepper seeds, whereas seeds of wild *C. annuum* var. *glabriusculum* do not germinate in constant darkness (Hernández-Verdugo *et al.*, 2001b).

B. Sexual reproduction

B.1. Pollination

31. *Capsicum* species are usually self-compatible (Onus and Pickersgill, 2004), and *C. annuum* is a partially self-pollinating crop (Allard, 1960; Rylski, 1986); wind or similar mechanical disturbance may enhance self-pollination (Raw, 2000; Kristjansson and Rasmussen, 1991). Outcrossing is associated with insect pollinators, less with wind (Odland and Porter, 1941; Tanksley, 1984a; Raw, 2000). The proportion of plants cross-pollinated depends on several factors and can range from 2 to 90% (Pickersgill, 1997); in many localities, cross-pollination is predominant. The effect of outcrossing on fruit set of *C. annuum* is significant. Nagarathnam and Rajamani (1963) obtained only 6-11% fruit set when flowers were isolated to self-pollinate. Erwin (1937) found that 46% of self-pollinated flowers set fruit, compared to 71% for flowers left to open-pollinate by bee activity. In field research *Capsicum* should be considered facultative cross-pollinating species (Odland and Porter, 1941; Tanksley, 1984a). Breeders and seed producers thus need to undertake precautionary measures to prevent uncontrolled cross-pollination (Bosland, 1993). To produce large amounts of genetically pure seeds, seed certification programmes employ isolation as the control mechanism. Isolation requirements may range from 400 m for the Certified class to 1.6 km for the Foundation class (NMCIA, 1992) but depend on local conditions, for example being 300 m in Hungary but perhaps requiring 2-3 km or more in Australia (Derera *et al.*, 2005).

32. The odourless flowers are visited by insects both for sugary nectar, which is mostly hexoses and low in daily amount (greatest on the day of anthesis), and also for their pollen (Rabinowitch *et al.*, 1993; Vogel, 1998; Roldán-Serrano and Guerra-Sanz, 2004; Raw, 2000). Solitary bees, honeybees, bumblebees, aphids and thrips are likely to transfer the pollen grains, especially those that obtain pollen by buzz pollination, shaking the anthers (Andrews, 1995; Raw, 2000; de Ruijter *et al.*, 1991; Kubišová and Háslbachová, 1991; Shipp *et al.*, 1994; Dag and Kamer, 2001; Kristjansson and Rasmussen, 1991).

B.2. Crossability and hybridisation

33. *Capsicum* species do not hybridise with species in other genera of the Solanaceae (Berke, 2000). Pepper breeding continues to be highly rewarding for the improvement of *Capsicum* (Poulos, 1994; Berke, 2000; Geleta and Labuschagne, 2004). Interspecific crossing between many *Capsicum* species has been tried experimentally (often repeatedly) for agronomic and taxonomic purposes (*cf.* Walsh and Hoot, 2001; Pickersgill, 1991, 1997; Onus and Pickersgill, 2004). Fertile hybridisations can occur between taxa within the *Capsicum annuum* complex to varying degrees (Jarret and Dang, 2004; Nwankiti, 1976; Kumar *et al.*, 1987; Panda *et al.*, 2004; Baral and Bosland, 2004), and also these species with *C. baccatum* but not with *C. pubescens*; Table 4 below gives a synopsis (*cf.* Yoon *et al.*, 2004). Similar interspecific spontaneous or natural hybrids of these species are difficult to ascertain, but infrequently surmised (Jarret and Dang, 2004; Rodriguez *et al.*, 1999). Their recognition is confounded by taxonomic uncertainty, the extensive variability from selection within the domesticated species for millennia to decades, and the plasticity of individual plants. Crossings between wild and semi-domesticated *C. annuum* var. *glabriusculum*, and between feral or weedy and domesticated *C. annuum* var. *annuum*, and these two complexes hybridising with each other, are probably a regular occurrence and vary in fertility (Jarret and Dang, 2004; Guzmán *et al.*, 2005; Hernández-Verdugo *et al.*, 2001a; Prince *et al.*, 1992; Pickersgill, 1971). Crossing also is

probable in many regions in the tropics between cultivated and feral *C. frutescens* (e.g. Yamamoto and Nawata, 2004, 2005; Symon, 1981; Wiggins and Porter, 1971).

Table 4. Crossability (including hybrid viability) of *Capsicum annuum* with other *Capsicum* in the three complexes of domesticated species (see Table 2)

<i>Capsicum annuum</i> (C _A) reciprocal crosses with other <i>Capsicum</i> species	
Interspecific parent and species complex	<i>Capsicum</i> sp. as female / male
<i>C. frutescens</i> (C _A)	(+) / +
<i>C. chinense</i> (C _A)	(+) / (+)
<i>C. galapagoense</i> (C _A)	† / +
<i>C. chacoense</i> (C _B or C _A)	0 / +
<i>C. baccatum</i> (C _B)	+ / +
<i>C. praetermissum</i> (C _B)	† / †
<i>C. tovarii</i> (C _B)	0 / 0
<i>C. pubescens</i> (C _P)	0 / 0
<i>C. cardenasii</i> (C _P)	0 / †
<i>C. eximium</i> (C _P)	0 / †

F₁ hybrids produce: viable seeds + , or some viable seeds (+) ; non-viable seeds † ; or no fruits and/or seeds 0 .

Source: after Pickersgill, 1971; IBPGR, 1983; Zijlstra *et al.*, 1991; Tong and Bosland, 1999

C. Asexual reproduction

34. The chili pepper plant can be propagated asexually by means of cuttings and grafting. Young cut shoots form whole independent plants with roots *in vitro* as well as in the field (Choi *et al.*, 1999; Shirai and Hagimori, 2004). Scions from chili pepper plants graft successfully on stocks of chili pepper (Chung and Choi, 2002) as well as tomato (Deloire and Héban, 1982). The grafted plants can set flowers and fruits. *Capsicum* grafting can induce genetic changes, which may provide variations of breeding value (Taller *et al.*, 1998, 1999).

SECTION VI. CROP PRODUCTION AND USE

35. Chili peppers are grown worldwide, either outside in fields or in greenhouses. The ability to produce a quality crop in such a wide range of climates and conditions has helped to make chili pepper a globally common crop. Because of the extensive cultivation, adaptation and variability of *C. annuum*, it is difficult to generalise to what is typical, and there is no single method for production (Bosland and Votava, 2000).

A. Environmental conditions

36. Chili pepper is a warm-season crop (Rodríguez-Rey *et al.*, 2000), and highly susceptible to frost. Watkins and Cantliffe (1983a) showed that at 25°C radicle emergence required 3.5 days, whereas at 15°C, 9 days were required. Seedling emergence from a soil depth of 1.2 cm took 8-9 days at temperatures from 25-35°C (Lorenz and Maynard, 1980), but was prevented below 15°C (Wien, 1997). The leaf unfolding rate of seedlings (based on maximum leaf count), which is also a measure of node and internode formation, was optimal at an average daily temperature of ~ 26°C (Si and Heins, 1996).

37. The plant is usually indeterminate and has continuous sympodial branching, with the individual branch systems apparently functioning as relatively autonomous integrated physiological units (Thomas and Watson, 1988; *cf.* de Swart *et al.*, 2004). For a high yield of good quality fruit, Bakker and van Uffelen (1988) found that mean air temperatures of 21-23°C were optimal during vegetative growth, followed by 21°C during fruit growth. The minimum temperature for growth and development is 18°C, below which growth is trivial, with plants in the 5-15°C range growing poorly (Sanders *et al.*, 1980). The most growth in the vegetative stage occurs at 25-27°C day temperature and 18-20°C night temperature (Dorland and Went, 1947; Bakker and van Uffelen, 1988). Day temperature lower than night temperature is detrimental to vegetative growth (as is a low night temperature of 12°C). Nonetheless, to grow compact greenhouse seedlings, higher night temperature is preferable (Si and Heins, 1996; Sysoyeva and Kharkina, 2000).

38. Maximum flower set occurs when day and night temperatures are between 21°C and 16°C. Flowers drop when the night temperature is above 24°C. Yields are high when the daily air temperature during fruit set ranges between 18-32°C. Fruits do not set when the mean daily temperature is above 32°C, or is below 16°C — or when cooler, the fruits are malformed (Olaireweju, 1988; Aloni *et al.*, 1999). Productivity is constrained by the adverse effects of high temperature on fruit set, and the detrimental influence of low temperature on fruit shape (Rylski and Spigelman, 1982; Rylski, 1973).

B. Agricultural practices

39. The ideal soil for producing chili pepper is deep, well-drained, medium-textured sandy loam or loam that holds moisture and has some organic matter. Plants can be started by direct seeding, or by transplanting after initial growth in trays (Bosland and Votava, 2000); the plants are started in greenhouses or hotbeds in many production areas, or in outdoor seedbeds in mild-climate areas. Chili pepper plants are transplanted when they are 6-8 weeks old. Prior to field planting, the plants should be hardened but not excessively.

40. Whether the field population is established by transplanting or direct seeded, the optimum crop is dependent upon row spacing and between-row spacing of the plants, and the type grown (Bosland and

Votava, 2000). Chili peppers require adequate amounts of most major and minor nutrients; the most-utilised are normally N and P. Plastic mulch maintains moisture in the soil; increases soil temperature and early yields; reduces weed populations, fertiliser leaching and soil compaction; and protects fruits from soil deposits and soil micro-organisms. Competition between weeds and chili peppers for nutrients, light and water is a serious problem in production (Lee and Schroeder, 1995). A successful weed control programme is essential for producing a healthy crop. Abiotic stresses include extreme temperatures, moistures, light, nutrients, pH, pollutants and pesticides.

41. Row covers or tunnel planting systems have been used for production in the field because of their effectiveness to alter microclimates. Chili pepper is sensitive to excessive water (Suh *et al.*, 1987). Irrigation is not necessary in areas with regular and ample rain, although it generally is essential in arid and semi-arid regions. Chili pepper is a shallow-rooted crop (González-Cervantes *et al.*, 2004). The amount and frequency of irrigation depend on soil type, bed type, plant size, humidity, wind, sunlight and prevailing temperatures. A limited supply of water during the rapid vegetative-growth period reduces the final yield (Beese *et al.*, 1982; Srinivasa-Rao and Bhatt, 1988; Sato *et al.*, 2003). Fruits grown under water deficit may have a higher concentration of capsaicin (Sung *et al.*, 2005).

42. Chili pepper plants can be made to behave perennially under greenhouse conditions, with environmental control carried out by air temperature regulation, supplemental light, and CO₂ enhancement as well. Regular removal of flowers leads to faster vegetative growth (Hall, 1977; Clapham and Marsh, 1987). In The Netherlands non-pungent chili peppers are greenhouse-grown on 1200 ha, and about a third of the workers develop an allergy to the pollen, which can be alleviated by introducing honeybees to remove pollen (Blacquièrre *et al.*, 2004).

C. Biotic stresses

43. Production can be diminished by various biotic stresses. Chili pepper is susceptible to diseases and pests that can be primary constraints on cultivation (Bosland and Votava, 2000; DeWitt and Bosland, 1993), and their control is one of the most important factors in producing a profitable crop. The diseases and pests usually reduce both quality and quantity of fruits.

44. Diseases from bacteria infecting the chili pepper plants include bacterial spot (*Xanthomonas campestris* pv. *vesicatoria*), bacterial canker (*Corynebacterium michiganense* or *Clavibacter michiganensis* subsp. *michiganensis*), bacterial soft rot (*Erwinia carotovora* pv. *carotovora*) and bacterial wilt (*Pseudomonas solanacearum* or *Ralstonia solanacearum*). The plants are susceptible to fungi which cause diseases such as anthracnose (*Colletotrichum* spp.), early blight (*Alternaria solani*), Cercospora leaf spot (*Cercospora capsici*), damping-off/seedling disease (*Pythium*, *Rhizoctonia*, *Fusarium*, etc.), Fusarium stem rot (*Fusarium solani*), grey mold (*Botrytis cinerea*), Phytophthora blight and root rot (*Phytophthora capsici*), powdery mildew (*Leveillula taurica* or *Oidiopsis taurica*), Rhizoctonia root rot (*Rhizoctonia solani*), Stemphylium leaf spot (*Stemphylium botryosum* f. sp. *capsicum*), gray leaf spot (*Stemphylium solani* and *S. lycopersici*), southern blight (*Sclerotium rolfsii*), Verticillium wilt (*Verticillium dahliae*) and white mold (*Sclerotinia sclerotium*). Among the many viruses affecting chili peppers are alfalfa mosaic alfamovirus (AMV), cucumber mosaic cucumovirus (CMV), beet western yellows luteovirus (BWYV), pepper mottle potyvirus (PepMoV), pepper veinal mottle potyvirus (PepVMoV), potato potyvirus Y (PVY), tobacco etch potyvirus (TEV), pepper mild mottle tobamovirus (PepMMoV), pepper ringspot tobamovirus (PepRSV), tomato spotted wilt tospovirus (TSWV), pepper golden mosaic bigeminivirus (PepGMV), pepper Huasteco bigeminivirus (PHV or PepHV), Texas pepper bigeminivirus (TPV) and beet curly top hybrigeminivirus (BCTV).

45. Production is affected by many insect pests such as cutworms, grubs (*Phyllophaga* spp.), flea beetles (*Epitrix* spp.), hornworms (*Manduca sexta* and *M. quinquemaculata*), grasshoppers, leafminers,

fruit worms (*Heliothis assulta* and *H. zea*, *Spodoptera* spp. armyworms, etc.), European corn borer (*Ostrinia nubilalis*), green peach aphid (*Myzus persicae*), melon or cotton aphid (*Aphis gossypii*), leafhoppers, stink bugs, tarnished plant bug (*Lygus lineolaris*), thrips, whiteflies, chili weevil (*Anthonomus eugenii*) and chili pepper maggot (*Zonosemata electa*), and by spider mites (*Tetranychus* spp.) and nematodes.

46. Chili pepper production is also influenced by physiological disorders such as flower-bud abscission and flower abscission, blossom-end rot, sunscald, abnormal fruit shape, colour spotting, and fruit cracking.

D. Experience and world statistics

47. Chili pepper is harvested at different fruit stages, depending on the final use. Fresh chili pods often are harvested at a physiologically immature (but horticulturally mature) stage. The dehydrated and mash industries use physiologically mature fruits, generally showing red colour.

48. Chili pungency is measured by determining the capsaicinoids content of the fruit, which can be accomplished by several industrial (laboratory) procedures, and as well by a subjective dilution-and-detection test (“taste test”) scored as Scoville Heat Units (Scoville, 1912; Korel *et al.*, 2002; Bosland and Votava, 2000; Krishna De, 2003; Reilly *et al.*, 2001). Physiologically, capsaicinoids cause the heat sensation by activating and then desensitising certain sensory nerve fibres, which is mediated *via* a receptor (VR1) in the pain pathway (Caterina and Julius, 2001; Bhave *et al.*, 2002). Culinary or medicinal results can be favourable (Rozin, 1990; Palevitch and Craker, 1995), whereas exposure to excessive amounts can range from avoidance behaviour to severe toxicity (Krenzelok and Provost, 1995).

49. The production of chili pepper for spice, vegetable, and other uses increases every year. It is estimated that it is annually cultivated on more than 1.5 million hectares, in numerous countries (FAO, 2003). Forty-six percent of production is in Asia (with China the principal producing country). Southern Europe is the second most important producing region, with 24% of world production. The countries with harvest area of more than 70,000 ha are China, India, Indonesia, Mexico, Korea, Nigeria, Ghana and Turkey.

SECTION VII. MODERN BIOTECHNOLOGY

50. Modern biotechnology can provide benefit to the chili pepper crop by genetic improvement against diseases and insect pests; for enhanced chemical composition, such as in carotenoids and capsaicinoids; and for improved marketing (Bosland and Votava, 2000; Ochoa-Alejo and Ramírez-Malagón, 2001). Development of a genetically transformed plant requires two key systems: the genetic transformation itself, *i.e.* transferring gene(s) of interest into host cells; and plant regeneration from the host cells with the inserted gene(s). Some other species in the family Solanaceae, such as tobacco (*Nicotiana tabacum*), tomato (*Lycopersicon esculentum*) and potato (*Solanum tuberosum*), have been used as model systems because of their successful transformation and regeneration. Chili pepper however has been recalcitrant, with application of molecular biotechnology lagging because there was not a reproducible, reliable and efficient system of transformation and regeneration (Ochoa-Alejo and Ramírez-Malagón, 2001), but these problems are now being overcome.

51. A few examples of efforts in the biotechnological development of *Capsicum* follow. Exposure to gamma radiation reduced the efficiency of chili pepper shoot regeneration (Sripichit *et al.*, 1988). Streptomycin-resistant shoots and whole plants from cotyledon explants were achieved by a regeneration system and chemical mutagenesis [with ethylmethane sulfonate (EMS)] (Subhash *et al.*, 1996). A high frequency of plastid-encoded antibiotic-resistant variants were isolated by Rao *et al.* (1997) from seeds and explants mutagenised with EMS or nitrosomethylurea. Dabauza and Peña (2001) improved the efficiency of organogenesis from seedling explants.

52. The first genetic transformation in chili pepper using modern molecular biotechnology was insertion of the genes for neomycin phosphotransferase and β -glucuronidase by means of *Agrobacterium tumefaciens* (Liu *et al.*, 1990); however, these transformed cells did not regenerate into whole plants. Since then, developments in technique for *C. annuum* have been reported steadily, for example, a stable system of *Agrobacterium*-mediated transformation and *in vitro* plant regeneration (Lee *et al.*, 1993), a refined protocol for transformation and regeneration (Manoharan *et al.*, 1998), a system for highly efficient transformation (40.8%) along with efficient regeneration (Li *et al.*, 2003), and the advances and refinements are continuing (Lee *et al.*, 2004b; Mihálka *et al.*, 2003).

53. Traits currently targeted for development of chili pepper include viral resistance to CMV, TEV and TMV (Cai *et al.*, 2003), pest resistance against oriental tobacco budworm (*Heliothis assulta*) (Kim *et al.*, 2002), altered fruit ripening, and prolonged shelf life. Diminishing cucumber mosaic virus disease has become a reality, after having developed the fertile transgenic plants with CMV resistance (Zhu *et al.*, 1996; Kim *et al.*, 1997). Genetically transformed *Capsicum annuum* with CMV resistance has been approved for commercialisation in China (Huang *et al.*, 2002).

SECTION VIII. REFERENCES

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