*Seed Science Research* (2000) **10**, 293–300

3rd International Workshop
Desiccation Tolerance and Sensitivity of Seeds
and Vegetative Plant Tissues
Itala Game Reserve
South Africa
January, 2000

# Relationship between seed desiccation sensitivity, seed water content at maturity and climatic characteristics of native environments of nine *Coffea* L. species

**Stéphane Dussert[1*], Nathalie Chabrillange[1], Florent Engelmann[2], François Anthony[3], Jacques Louarn[4] and Serge Hamon[1]**

[1]IRD, GeneTrop, BP 5045, 34032 Montpellier Cedex 1, France; [2] IPGRI, Via delle Sette Chiese 142, 00145 Rome, Italy; [3]CATIE, Apartado 59, 7170 Turrialba, Costa Rica; [4]IRD, BP 434 Man, Côte-d'Ivoire

## Abstract

A broad variability for seed desiccation sensitivity, as quantified by the water content and the water activity at which half of the initial viability is lost, has been previously observed within nine African coffee species. In order to investigate if these different degrees of desiccation sensitivity correspond to an adaptive trait, additional data, such as the duration of seed development and seed water content at maturity, were measured for these species, and the relationships between these parameters and some climatic characteristics of their specific native environments were investigated. Since flowering in all coffee species occurs only a few days after the main rainfall marking the end of the dry season, simulations could be made, based on the continuous sequences of rainfall data compiled in databases of nine climatic stations, chosen for their appropriate location in the collecting areas. The simulations revealed a highly significant correlation between the duration of seed development and that of the wet season. Consequently, mature seeds are shed at the beginning of the following dry season. Moreover, the mean number of dry months that seeds have to withstand after shedding was significantly correlated with the parameters used to quantify seed desiccation sensitivity. By contrast, seed moisture content at maturity was not correlated with the level of seed desiccation tolerance. All these results are discussed on the basis of more detailed descriptions of the natural habitats of the coffee species studied.

**Keywords: Coffee, *Coffea*, climate, desiccation sensitivity, development, drought, seed**

## Introduction

Differences in seed desiccation sensitivity between species of the sub-genus *Coffea* have been reported recently in three different studies (Hong and Ellis, 1995; Dussert *et al*., 1999a; Eira *et al*., 1999). Even if the post-harvest handling, desiccation, rehydration and germination procedures employed in these studies differed, the overall ranking of the coffee species studied as regards their level of desiccation sensitivity was the same in these three investigations, thus supporting the hypothesis of the genetic basis of these interspecifc differences. Therefore, coffee species appear to represent an appropriate plant material in which to investigate whether the variability in seed desiccation sensitivity observed within a genus corresponds to adaptations to different environments.

Almost 20 years ago, Roberts and King (1980) suggested there is an association between plant ecology and seed storage behaviour. Since then, significant associations between the level of desiccation sensitivity and the typology of natural habitat (e.g. tropical/temperate) have been established (von Teichman and van Wyk, 1994; Hong and Ellis, 1996), although investigations on this topic are rare. For coffee species, the variability observed for seed desiccation sensitivity (Hong and Ellis, 1995; Eira *et al*., 1999) has been associated with qualitative differences in the nature of the native environments of the species studied. For example, Hong and Ellis (1995) reported that *Coffea arabica* shows intermediate seed storage behaviour and is native to the dry highlands of Ethiopia, while *Coffea liberica* shows recalcitrant seed storage behaviour and originates from the humid regions of Africa. Although these associations constitute a sound basis for supporting the hypothesis

---

*Correspondence
Fax: +33–4-67–54–78–00
Email: dussert@mpl.ird.fr

that the differences observed in desiccation sensitivity could correspond to an adaptative trait, they did not establish that the duration of seed exposure to drought varies between coffee species. Moreover, statistical relationships between parameters quantifying the level of desiccation sensitivity and those describing climatic characteristics of native environments still do not exist.

The subgenus *Coffea* L. includes more than 90 taxa (Bridson and Verdcourt, 1988). All species of this subgenus are native to the inter-tropical forests of Africa, Madagascar and the islands of the Indian Ocean (Mascareignes and Comores Islands). Since 1960, IRD scientists have been involved in collecting wild species of the sub-genus *Coffea* (Berthaud and Charrier, 1988). The observation of coffee trees in their native environment constitutes a precious source of information on the reproductive biology of these species. Moreover, all collectors have noticed specific plant adaptations to rainfall/drought, altitude and soil types (Charrier and Berthaud, 1985). In addition, on the basis of *in situ* observations carried out over several successive years, Berthaud (1986) has provided valuable information on the organisation of some wild populations of several coffee species and on how genes flow among these populations. Although these studies did not aim at obtaining information on coffee seed ecology, some of the *in situ* observations reported by this author are particularly interesting: for example, Berthaud (1986) observed that, in a wild population of *Coffea stenophylla* located in Côte-d'Ivoire, seeds became mature and were shed just at the beginning of the dry season. This author thus wondered how seeds could survive until water became again available, since at that time coffee seeds were thought to be truly recalcitrant.

The desiccation sensitivity of seeds of some of the wild coffee species collected by IRD has been studied recently (Dussert *et al.*, 1999a). Since the exact origin of the material studied and the corresponding rainfall data were available, simulations were carried out to investigate if differences in the level of seed desiccation tolerance among these species were correlated with differences in the duration of seed exposure to drought in their native environments.

## Materials and methods

### *Plant material*

In the case of *Coffea brevipes* Hiern, *C. canephora* Pierre, *C. eugenioides* Moore, *C. humilis* Chevallier, *C. liberica* Hiern, *C. pocsii* Bridson, *C. pseudozanguebariae* Bridson and *C. stenophylla* G. Don., wild coffee trees from which seeds were collected for desiccation studies originated from Cameroon, Côte-d'Ivoire, Central African Republic, Kenya and Tanzania (Table 1). This germplasm is conserved in two base field collections located in Côte-d'Ivoire (IRD-IDEFOR, Divo and IRD, Man). For each species, only one to four wild populations were studied, which were located within restricted geographical areas (Fig. 1). Passport data of the genotypes studied (20 to 40 genotypes per species) were extracted from a database, BaseCafé (Anthony, 1992), containing passport, management and evaluation data for the two coffee collections maintained in Côte-d'Ivoire. The trees studied of *C. arabica* var. typica are maintained in CATIE, Turrialba, Costa Rica. The exact origin of the variety Typica is unknown, but it was established through molecular studies that it originates from the eastern part of the natural distribution area of the species, which is the south-west of Ethiopia (Fig. 1; Lashermes *et al.*, 1996).

### *Seed desiccation sensitivity*

Seed desiccation sensitivity of the nine coffee species has been previously studied by measuring the production of normal seedlings after equilibration of seeds over various saturated salt solutions (Dussert *et al.*, 1999a). Seed desiccation sensitivity was quantified by the water content and the corresponding water

**Table 1.** Country of origin of the nine species studied, type of forest in which coffee trees were collected, and corresponding bibliographic references. CAR: Central African Republic.

| Species | Country | Forest type | Reference |
|---|---|---|---|
| *C. arabica* | Ethiopia | Highland forest | Lashermes *et al.* (1996) |
| *C. brevipes* | Cameroon | Rainforest | Anthony *et al.* (1985) |
| *C. canephora* | CAR | Semi-deciduous forest | Berthaud and Guillaumet (1978) |
| *C. eugenioides* | Kenya | Highland forest | Berthaud *et al.* (1980) |
| *C. humilis* | Côte-d'Ivoire | Rainforest | Berthaud (1986) |
| *C. liberica* | CAR | Gallery forest | Berthaud and Guillaumet (1978) |
| *C. pocsii* | Tanzania | Forest patches in woody savannah | Berthaud *et al.* (1983) |
| *C. pseudozanguebariae* | Kenya | Coastal dry forest on coral rag | Berthaud *et al.* (1980) |
| *C. stenophylla* | Côte-d'Ivoire | Semi-deciduous forest | Berthaud (1986) |

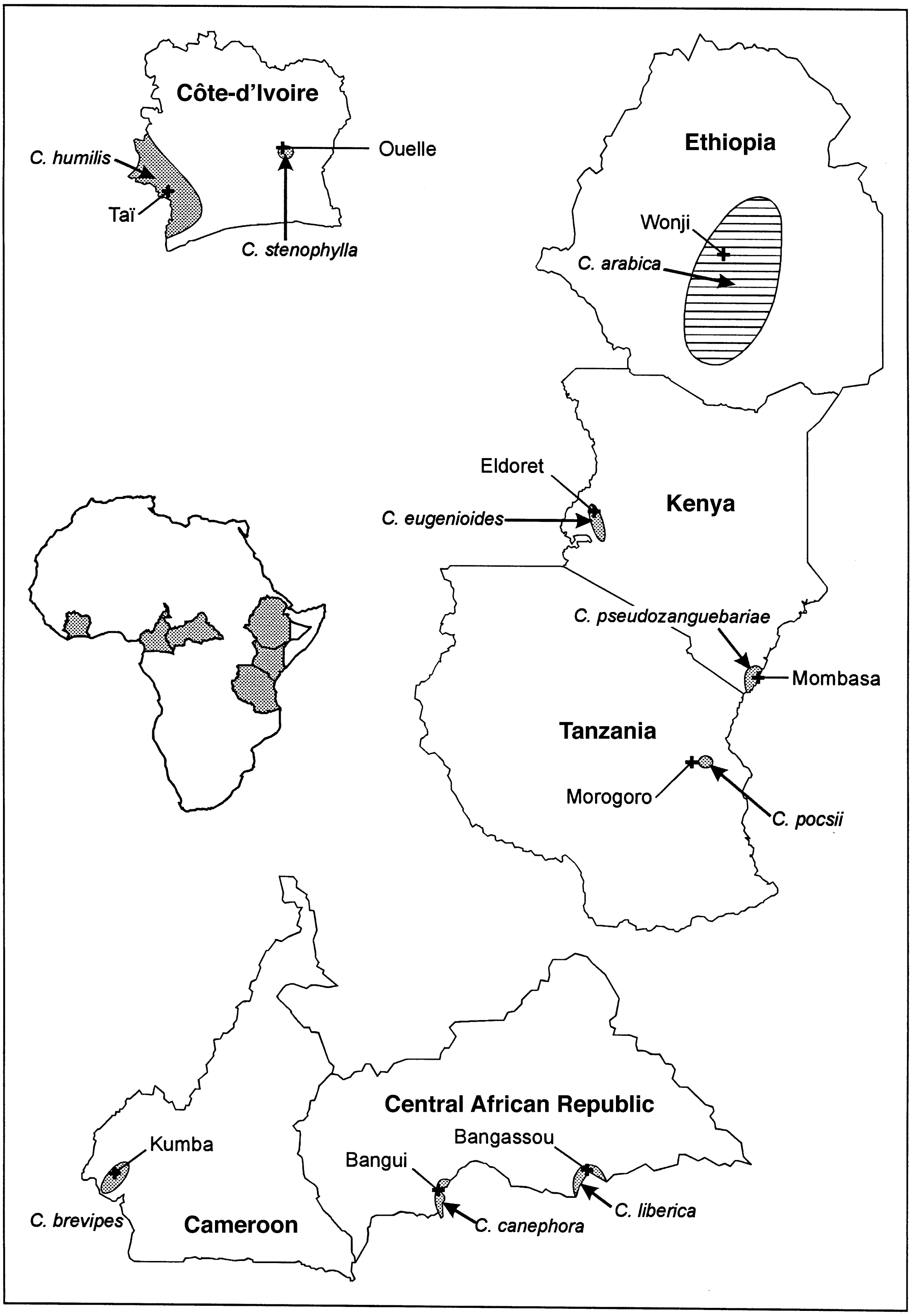

**Figure 1.** Geographical origin of the plant material studied (grey areas correspond to the exact origin of wild germplasm collected by IRD; for *C. arabica*, the hatched area corresponds to the supposed origin of the variety Typica as suggested by Lashermes *et al.* (1996) and location of the nine sources of monthly rainfall data (✚).

activity at which half of the initial viability is lost, $WC_{50}$ and $a_{w50}$, respectively, as previously described in Dussert *et al.* (1999a).

### Seed development duration and seed water content at maturity

For all species except *C. arabica*, seed development duration was measured on three to five trees randomly chosen among those from which seeds had been collected for previous desiccation studies. For *C. arabica*, the duration of seed development could not be measured at CATIE (Costa Rica) since the absence of a true dry season in this location renders it unsuitable for the evaluation of this trait (Anthony, personal communication). This parameter was thus measured in Côte-d'Ivoire with wild accessions collected by IRD within the same area of origin as the variety Typica (i.e. in south Ethiopia). The low intraspecific variability for seed desiccation sensitivity observed in *C. arabica* (Ellis *et al.*, 1990; Eira *et al.*, 1999) rendered this approximation acceptable.

On the day of flowering, one branch was chosen on each tree for its high number of opened flowers; all floral buds not opened on this branch were eliminated by hand. Weekly observations of all the branches studied allowed the determination of seed development duration as estimated by the number of weeks between the day of flowering on selected branches and the time when fruit maturity was reached. Fruits were considered mature when a specific change in colour had occurred in all those on the branches studied. Since shedding occurs very rapidly after this change in fruit colour in coffee species, ten fruits were harvested at this stage on each branch studied for the determination of seed water content at maturity.

### Climatic characteristics of native environments

Two sources of monthly rainfall data were used: the Global Historical Climatology Network (Vose *et al.*, 1992) and IRD rainfall database (CIEH/ORSTOM, 1973–1990). Nine climatic stations were chosen in these two databases for their location in the areas of origin of the plant material studied (Fig. 1, Table 2). Two variables were directly calculated from the data available for 25 to 90 years: the mean annual rainfall and the mean duration of the rainy season. The duration of a rainy season was estimated by the number of successive months for which rainfall was higher than 50 mm. At Morogoro, Tanzania and Mombasa, Kenya, two rainy seasons were observed in some years. In such cases, both were taken into account for calculating the mean duration of the rainy season.

### Simulation of reproductive cycle

For each species, simulations were performed to determine the mean duration of seed exposure to drought after shedding. Flowering biology of all coffee species shows very peculiar characteristics (Berthaud, 1986; Anthony, 1992; Akaffou, 1999).

- Flowering may occur after only 1–2 months of drought, which is necessary for the induction of floral buds (this characteristic is one of the main limiting factors for selecting areas in which coffee can be grown).
- Flowering is induced by the first abundant rainfall marking the end of the dry season.
- The number of days between the inducing rainfall and flowering is genetically controlled and varies from 6 to 9 days, depending on the species.
- Flowers remain open for 1 day only.

Using our knowledge of the flowering biology of coffee species presented above and the rainfall data collected in the different locations studied, the flowering date could be estimated for each species. It was indicated on the graph presenting the monthly rainfall data of the relevant station, as illustrated on Fig. 2 for *C. humilis*. The duration of the seed development

**Table 2.** Climatic stations located within origin areas of the plant material studied: name, country and altitude of the station, mean annual rainfall, and number ($n$) of continuous years for which monthly rainfall data were available in the source database. CAR: Central African Republic. GHCN: Global Historical Climatology Network.

| Species | Station | Country | Altitude (m) | Annual rainfall (mm) | $n$ | Source |
|---|---|---|---|---|---|---|
| *C. arabica* | Wonji | Ethiopia | 1500 | 739 | 25 | GHCN |
| *C. brevipes* | Kumba | Cameroon | 140 | 2412 | 32 | IRD |
| *C. canephora* | Bangui | CAR | 365 | 1525 | 58 | GHCN |
| *C. eugenioides* | Eldoret | Kenya | 2120 | 1129 | 46 | GHCN |
| *C. humilis* | Taï | Côte-d'Ivoire | 123 | 1924 | 45 | IRD |
| *C. liberica* | Bangassou | CAR | 499 | 1733 | 32 | GHCN |
| *C. pocsii* | Morogoro | Tanzania | 526 | 892 | 53 | GHCN |
| *C. pseudozanguebariae* | Mombasa | Kenya | 57 | 1149 | 90 | GHCN |
| *C. stenophylla* | Ouelle | Côte-d'Ivoire | 230 | 1005 | 31 | IRD |

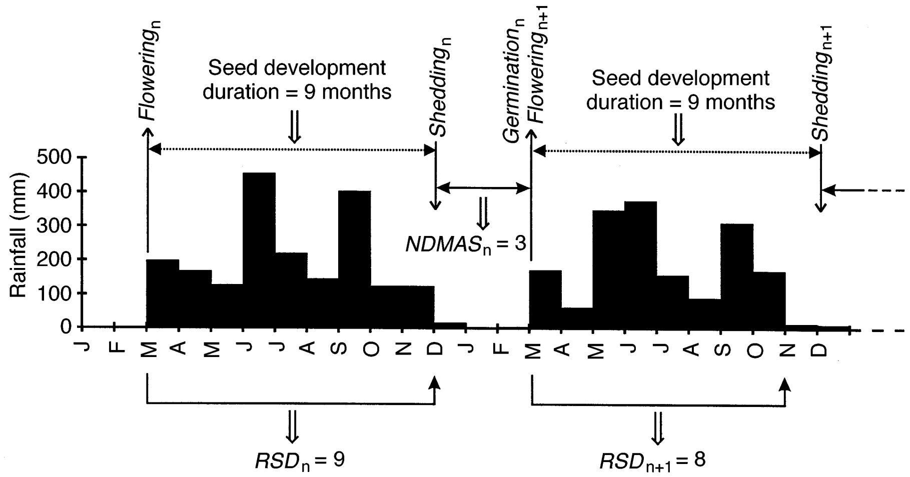

**Figure 2.** Example of a simulation of the reproductive cycle for *C. humilis*. The graph presents the rainfall data recorded for two successive years at Taï, Côte-d'Ivoire. The following additional information is indicated on the graph: date of flowering, duration of seed development, date of shedding, duration of rain season (*RSD*) and number of dry months after shedding (*NDMAS*).

of each species, which had been measured previously, was then added to the same graph, thus allowing the determination of both the time of shedding and the number of dry months after shedding.

## Results

### Relationship between duration of development, water content at maturity and desiccation sensitivity of seeds of nine coffee species

A very broad variability for seed development duration was observed among the nine coffee species studied (Table 3): it ranged from 2.1 months with *C. pocsii* to 10.6 months with *C. canephora* and *C. liberica*. These species showed moderate differences in seed water content at maturity: it varied from 0.84 g $H_2O$ $g^{-1}$ dw with *C. pseudozanguebariae* to 1.39 g $H_2O$ $g^{-1}$ dw with *C. brevipes*, and was approx. 1 g $H_2O$ $g^{-1}$ dw for most of the other species studied.

No significant correlation was found between the level of desiccation sensitivity of coffee seeds, as quantified by the water content or the water activity at which half of the initial viability was lost, and the duration of seed development or the seed water content at maturity (Table 4).

### Relationship between duration of development, desiccation sensitivity of seeds of nine coffee species and climatic characteristics of their native environments

A very highly significant correlation ($P = 0.000001$; $R^2 = 0.98$) was found between the duration of seed development of the nine coffee species studied and the duration of the rainy season in their native environments (Fig. 3). As flowering in all coffee

**Table 3.** Seed development duration (*SDD*), seed water content at maturity ($WC_m$), water content at which 50% of initial viability was lost ($WC_{50}$) and corresponding water activity ($a_{w50}$) for the nine coffee species studied (nd: not determined).

| Species | *SDD* (months) | $WC_m$ (g $H_2O$ $g^{-1}$ dw) | $WC_{50}$ | $a_{w50}$ |
|---|---|---|---|---|
| *C. arabica* | 6.9 | 1.05 | 0.109 | 0.444 |
| *C. brevipes* | 10.5 | 1.39 | 0.203 | 0.766 |
| *C. canephora* | 10.6 | 0.97 | 0.170 | 0.692 |
| *C. eugenioides* | 7.8 | 0.91 | 0.110 | 0.409 |
| *C. humilis* | 8.9 | 1.09 | 0.382 | 0.920 |
| *C. liberica* | 10.6 | 0.99 | 0.288 | 0.874 |
| *C. pocsii* | 2.1 | 1.23 | 0.153 | 0.744 |
| *C. pseudozanguebariae* | 2.3 | 0.84 | 0.056 | 0.293 |
| *C. stenophylla* | 8.5 | nd | 0.158 | 0.670 |

**Table 4.** Results of linear regression analysis for the nine coffee species studied between the two parameters describing seed desiccation sensitivity, $WC_{50}$ and $a_{w50}$, and climatic characteristics of natural habitats (number of dry months following seed shedding, annual rainfall) and seed water content at maturity: proportion of variance explained by the linear regression model $R^2$ and probability $P$. $^{NS}$non significant, *significant, **highly significant.

| | | $WC_{50}$ | $a_{w50}$ |
|---|---|---|---|
| Seed development duration | $P$ | 0.1252 $^{NS}$ | 0.1506 $^{NS}$ |
| | $R^2$ | 0.3021 | 0.2711 |
| Seed water content at maturity | $P$ | 0.4564 $^{NS}$ | 0.1508 $^{NS}$ |
| | $R^2$ | 0.0955 | 0.3111 |
| Number of dry months after shedding | $P$ | 0.0318 * | 0.0088** |
| | $R^2$ | 0.5051 | 0.6486 |
| Annual rainfall | $P$ | 0.0592 $^{NS}$ | 0.0872 $^{NS}$ |
| | $R^2$ | 0.4197 | 0.3607 |

species coincides with the beginning of the rainy season, the main consequence of this is that seed shedding coincides with the end of the rainy season.

Although the probabilities observed were close to the $P$=0.05 level of significance, the levels of seed desiccation sensitivity of the coffee species studied and the mean annual rainfall of their native environments were not correlated (Tables 2 and 4). By contrast, the two parameters used for quantifying seed desiccation sensitivity, $WC_{50}$ and $a_{w50}$, were significantly correlated with the mean number of dry months following seed shedding, as estimated by simulations of flowering, seed development and shedding events on sequences of rainfall data (Table 4; Fig. 4).

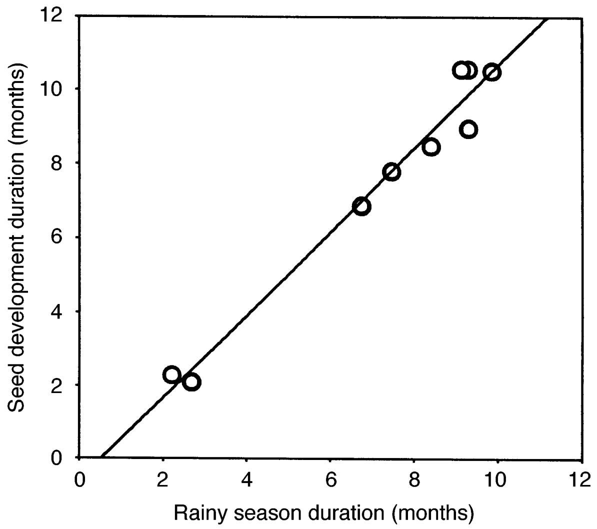

**Figure 3.** Correlation between the duration of the rainy season in native environments of the nine coffee species studied and the duration of seed development in these species.

## Discussion

The coffee species studied showed a very broad variability in terms of seed development duration. The values obtained in the present study are very similar to those observed by various authors (Cambrony, 1988; Anthony, 1992; Akaffou, 1999). The very low effect of environment on the duration of seed development in coffee species has been well established at the interspecific level (Cambrony, 1988; Akaffou, 1999). Thus, even if seed desiccation sensitivity and seed development duration were not

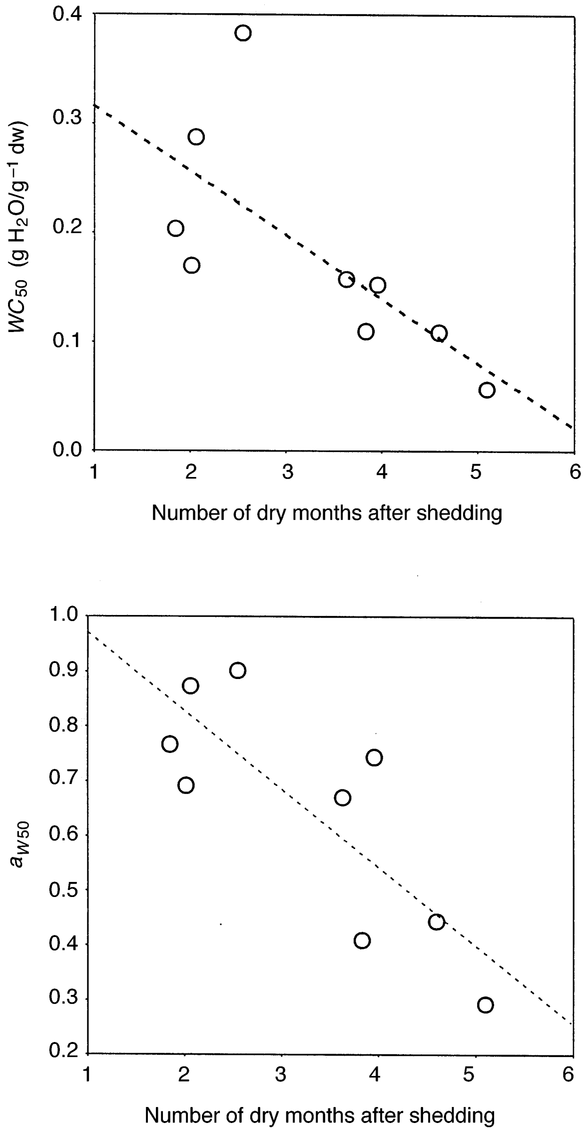

**Figure 4.** Correlation between the number of dry months following seed shedding and the two parameters used to describe seed desiccation sensitivity in the nine coffee species studied: water content at which half of the initial viability was lost, $WC_{50}$, and corresponding water activity, $a_{w50}$.

measured using the same plant material for *C. arabica*, it can be assumed that the main results of the present study would not have been different if these two traits had been evaluated with seeds coming from the same trees.

No significant correlation was found between the duration of seed development and the level of seed desiccation tolerance in coffee species. This had been suggested previously by Eira *et al*. (1999) in a study on tolerance to desiccation of seeds of *C. arabica*, *C. canephora*, *C. congensis*, *C. liberica* and *C. racemosa*. The independence between these two parameters has to be associated with the similarity of values of seed water content at maturity among coffee species. Indeed, a higher level of desiccation tolerance could have been associated with a longer duration of seed development if it would have included a desiccation step, as is the case in orthodox seeds (Vertucci and Farrant, 1995). The changes in water content in coffee seeds throughout their development were not measured in the present study, but it can be assumed that none of the coffee species studied shows a true desiccation step during seed development.

A significant correlation was found between the duration of seed development and that of the wet season in native environments of the nine coffee species studied. This result, associated with our knowledge of the peculiar flowering biology of coffee species, allows us to suggest that water availability during the entire duration of seed development is one of the main characteristics of the reproductive strategy of all coffee species. This characteristic implies an adaptation of seeds to another challenge: since seed shedding occurs at the beginning of the dry season, as observed *in situ* by Berthaud (1986), seeds have to withstand drought periods of various lengths until water again becomes available for germination. On the basis of the simulations performed, it appeared that the level of seed desiccation tolerance was significantly correlated with the number of dry months following seed shedding. It can thus be suggested that, with coffee, a higher level of tolerance to desiccation corresponds to an adaptation to drought. Data obtained by Eira *et al*. (1999) for two coffee species which were not included in our study substantiate this result: *C. racemosa*, which possesses a seed development duration of about 2 months and originates from Mozambique where the rainy season is very short, was found to be highly tolerant to desiccation, and *C. congensis*, which is endemic to the banks of rivers of central Africa, showed a tolerance to desiccation similar to that of *C. canephora*.

The utilisation of quantitative parameters for describing both seed desiccation sensitivity and climatic characteristics of native environments allows the use of a statistical approach to the ecology of seed desiccation tolerance. The qualitative information found in collecting reports provides very interesting descriptions of wild coffee trees in their native environments that reinforce the quantitative results obtained in the present study. Berthaud (1986) found some wild populations of *C. canephora*, *C. liberica* and *C. stenophylla* on the same hills in Côte-d'Ivoire, but *C. stenophylla* was found only on tops of hills, whereas *C. canephora* and *C. liberica* were located only at the bottom. Interestingly, this author reported that in West Africa a gradient of moisture exists from the top of the hills to the bottom, the top constituting a drier environment due to better drained soils. In Côte-d'Ivoire, Berthaud (1986) emphasised that *C. humilis*, which is endemic to the rainforest of south-west Côte-d'Ivoire, grows only on thalwegs (valley floors) or on the banks of back-waters and pools, which correspond to the most humid micro-areas of the rainforest. During a collecting mission in Uganda, Thomas (1944) noticed that '*C. eugenioides* appears to withstand drought better than any of the other wild coffees of Uganda' (*C. canephora* and *C. liberica*) since 'it is restricted to the higher slopes where there is a rapid percolation through the stony soils' and 'all the plants are wilted during the dry seasons'. This author reported that, in some localities, *C. canephora* and *C. eugenioides* were found close to each other; however, *C. eugenioides* grew only in the drier areas near the edge of the forest whereas *C. canephora* was restricted to the humid hollows located in the centre of the forest.

The only approach which could confirm the adaptative feature of the level of seed desiccation tolerance in coffee species would be to carry out new observations *in situ*. Indeed, the simulations performed in the present study did not take into account many parameters that could be involved in the desiccation of seeds in their natural environment, such as soil and surface characteristics, temperature and light conditions. The need for a more detailed characterisation of specific habitats is emphasised by the fact that a global parameter such as the mean annual rainfall appeared to be a poor indicator of the level of seed desiccation sensitivity. Unfortunately, the possibility of visiting the original sites where these wild coffee species were collected is remote because of the intense deforestation occurring in many parts of Africa.

Only two African coffee species, *C. canephora* and *C. liberica*, show a very large area of natural distribution. They are found from the west coast to the east coast of Africa, from Guinea to Sudan, and from the north to the south, from Cameroon to Angola (Berthaud, 1986). Various environments exist within such a large area of distribution, notably regarding the duration of the dry season. Since these species show a broad phenotypic variability, particularly with regard to seed development duration (Leroy *et al.*, 1993; Dussert *et al.*, 1999b), drought tolerance of plants (Leroy *et al.*, 1993) and large genetic diversity (Dussert *et al.*, 1999b), it can be expected that they also show adaptative variations for tolerance of seeds to desiccation. Intraspecific variability in seed desiccation sensitivity has been observed by Eira *et al.* (1999) in *C. liberica*. Moreover, the parallel between the very low variability observed for seed desiccation sensitivity between *C. arabica* varieties (Ellis *et al.*, 1990; Eira *et al.*, 1999) and the very low genetic diversity of this species (Lashermes *et al.*, 1996) must be emphasised. Further investigations on the intraspecific variability in seed desiccation sensitivity should, thus, be carried out using the available diversity of wild *C. canephora* and *C. liberica* collected in various environments.

## Acknowledgements

The authors gratefully acknowledge Thierry Valéro (IRD) for the development of software allowing user-friendly queries of the GHCN database.

## References

**Akaffou, D.S.** (1999) Etude des hybrides interspécifiques entre *Coffea pseudozanguebariae* et *C. liberica* et analyse des possibilités d'introgression. PhD Thesis, University of Abidjan, Côte-d'Ivoire.

**Anthony, F.** (1992) *Les ressources génétiques des caféiers: collecte, gestion d'un conservatoire et évaluation de la diversité génétique*. Paris, IRD Edition.

**Anthony, F., Couturon, E. and de Namur, C.** (1985) Les caféiers sauvages du Cameroun: résultats d'une mission de prospection réalisée par l'ORSTOM en 1983. pp. 495–505 *in Proceedings of the 11th ASIC Symposium*, Lomé, Togo.

**Berthaud, J.** (1986) *Les ressources génétiques pour l'amélioration des caféiers africains diploïdes*. Paris, IRD Edition.

**Berthaud, J. and Charrier, A.** (1988) Genetic resources of *Coffea*. pp. 1–42 *in* Clarke, R.J.; Macrae, R. (Eds) *Coffee, Vol. 4, Agronomy*. London, Elsevier Applied Science.

**Berthaud, J. and Guillaumet, J.L.** (1978) Les caféiers sauvages en Centrafrique. Résultats d'une mission de prospection (janvier-février 1975). *Café Cacao Thé* **22**, 171–186.

**Berthaud, J., Anthony, F. and Lourd, M.** (1983) Les caféiers sauvages de Tanzanie. Résultats d'une mission de prospection effectuée du 5 mars au 11 avril 1982. *Café Cacao Thé* **27**, 245–258.

**Berthaud, J., Guillaumet, J.L., Le Pierrès, D. and Lourd, M.** (1980) Les caféiers sauvages du Kenya: prospection et mise en culture. *Café Cacao Thé* **24**, 101–112.

**Bridson, D.M. and Verdcourt, B.** (1988) *Coffea*. pp. 703–723 *In* Polhill, R.M. (Ed.) *Flora of tropical East Africa–Rubiaceae (Part 2)*. Rotterdam, Brookfield, Balkema.

**Cambrony, H.R.** (1988) Arabusta and other interspecific hybrids. pp. 263–292 *in* Clarke, R.J.; Macrae, R. (Eds) *Coffee*. Vol. 4. *Agronomy*. London, Elsevier Applied Science.

**Charrier, A. and Berthaud, J.** (1985) Botanical classification of coffee. pp. 13–47 *in* Clifford, M.N.; Willson, K.C. (Eds) *Coffee. Botany, biochemistry and production of beans and beverage*. Westport, Connecticut, AVI Publishing.

**CIEH/ORSTOM** (1973–1990) Précipitations journalières de l'origine des stations à 1990. Paris, France, IRD Editions.

**Dussert, S., Chabrillange, N., Engelmann, F. and Hamon, S.** (1999a) Quantitative estimation of seed desiccation sensitivity using a quantal response model: application to nine species of the genus *Coffea* L. *Seed Science Research* **9**, 135–144.

**Dussert, S., Lashermes, P., Anthony, F., Montagnon, C., Trouslot, P., Combes, M.C., Berthaud, J., Noirot, M. and Hamon, S.** (1999b) Le caféier, *Coffea canephora*. pp. 175–194 *in* Hamon, P.; Seguin, M.; Perrier, X.; Glaszmann, J.C. (Eds) *Diversité génétique des plantes tropicales cultivées*. Montpellier, France, CIRAD.

**Eira, M.T.S., Walters, C., Caldas, L.S., Fazuoli, L.C., Sampaio, J.B. and Dias, M.C.** (1999) Tolerance of *Coffea* spp. seeds to desiccation and low temperature. *Revista Brasileira de Fisiologia Vegetal* **11**, 97–105.

**Ellis, R.H., Hong, T.D. and Roberts, E.H.** (1990) An intermediate category of seed storage behaviour? I. Coffee. *Journal of Experimental Botany* **41**, 1167–1174.

**Hong, T.D. and Ellis, R.H.** (1995) Interspecific variation in seed storage behaviour within two genera–*Coffea* and *Citrus*. *Seed Science and Technology* **23**, 165–181.

**Hong, T.D. and Ellis, R.H.** (1996) *A protocol to determine seed storage behaviour*. Rome, Italy, International Plant Genetic Resources Institute.

**Lashermes, P., Trouslot, P., Anthony, F., Combes, M.C. and Charrier, A.** (1996) Genetic diversity for RAPD markers between cultivated and wild accessions of *Coffea arabica*. *Euphytica* **87**, 59–64.

**Leroy, T., Montagnon, C., Charrier, A. and Eskes, A.B.** (1993) Reciprocal recurrent selection applied to *Coffea canephora* Pierre. I. Characterization and evaluation of breeding populations and value of intergroup hybrids. *Euphytica* **67**, 113–125.

**Roberts, E.H. and King, R.H.** (1980) The characteristics of recalcitrant seeds. pp. 1–5 *in* Chin, H.F.; Roberts, E.H. (Eds) *Recalcitrant crop seeds*. Kuala Lumpur, Tropical Press.

**Thomas, A.S.** (1944) The wild coffees of Uganda. *Empire Journal of Experimental Agriculture* **12**, 1–12.

**Vertucci, C.W. and Farrant, J.M.** (1995) Acquisition and loss of desiccation tolerance. pp. 237–271 *in* Kigel, J.; Galili, G. (Eds) *Seed development and germination*. New York, Marcel Dekker.

**von Teichman, I. and van Wyk, A.E.** (1994) Structural aspects and trends in the evolution of recalcitrant seeds in dicotyledons. *Seed Science Research* **4**, 225–239.

**Vose, R.S., Schmoyer, R.L., Steurer, P.M., Peterson, T.C., Heim, R., Karl, T.R. and Eischeid, J.** (1992) The global historical climatology network: long-term monthly temperature, precipitation, sea-level pressure, and station pressure data. Oak Ridge, Tenessee, Carbon Dioxide Information Analysis Center.

Received 10 January 2000
Accepted after revision 9 May 2000