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# Corn poppy (*Papaver rhoeas* L.) resistance to ALS inhibiting and 2,4-D herbicides in Moroccan and Tunisian rainfed wheat fields

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**Abstract:** Corn poppy (*Papaver rhoeas* L.) is one of the most problematic weed species, mainly in rainfed Moroccan and Tunisian cereal crops. The overuse of acetolactate synthase (ALS) inhibiting and/or auxinic herbicides led to the spread of corn poppies resistant to both chemical families in this region. In order to identify and understand the selection drivers of resistance, appropriate characterisation of the resistance profile is necessary. Two experiments were carried out: biological sensitivity tests with ALS inhibiting herbicides (tribenuron-methyl and florasulam) and auxinic herbicides (2,4-D) were carried out with populations sampled in the field where the herbicide failure was observed. Bioassay tests confirmed resistance in all studied populations with an average frequency of 75.13, 30.81, 33.17 and 11.52% with tribenuron, florasulam, 2,4-D and florasulam + 2,4-D, respectively. Corn poppy sampled from both countries exhibited similar frequencies within populations for each tested herbicide. The molecular analysis was conducted with next-generation sequencing (Illumina), allowing massive, precise and rapid sequencing regions of the ALS gene carrying resistance codons. Using this technology, ALS mutant alleles were found in all populations at frequencies ranging from 1.4% to 63.3%, with an average of 16.7%. This study highlights the need to elucidate resistance mechanisms to understand herbicide responses and develop effective strategies for managing resistant corn poppy in rainfed cereals as an essential step to maintain the effectiveness of these molecules as long as possible.

**Keywords:** broadleaved weeds; weed control; mutation; herbicide resistance

Corn poppy (*Papaver rhoeas* L.) is one of the most common broadleaved weeds infesting cereal crops across Europe, especially in the southern areas with Mediterranean climates (Caballero 2016). Due to its geographical vicinity but not only, corn poppy became abundant in both northern Morocco and Tunisia, causing large yield losses in cereal crops (Bouhache 2018, 2020, Chtourou et al. 2024, Tanji 2024). Corn poppy is an annual, insect-pollinated and diploid species ($2n = 14$) with high self-incompatibility (Délye et al. 2011). This species' ability to persist, germinate, and compete with winter wheat necessitates herbicide application as the most effective control method. However, the intensive use of acetolactate synthase (ALS)-inhibiting herbicides and auxin mimics has led to corn poppy resistant to both herbicide modes of action (MoA) in Tunisia and Morocco (Bouhache 2018, Chtourou et al. 2024).

Herbicide resistance is classified into two mechanisms: (*i*) target-site resistance (TSR): caused by muta-

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tions in the gene encoding the herbicide target, leading to structural and functional changes at the binding site (Powles and Yu 2010, Caballero et al. 2017); (*ii*) non-target-site resistance (NTSR): encompasses various mechanisms that prevent herbicide molecules from reaching their target proteins (Scarabel et al. 2015, Suzukawa et al. 2021). These mechanisms include reduced herbicide uptake as well as translocation, decreased activation, and increased sequestration or metabolism rates (Délye et al. 2013). Seven alleles of TSR at two codons (Pro197 and Trp574) have been reported in corn poppy to date (Kati et al. 2019, Stankiewicz-Kosyl et al. 2023). Several mechanisms of NTSR have been investigated over the years for ALS-inhibiting herbicides (Jugulam et al. 2019), and many of these studies have mostly identified the enhanced expression or upregulation of cytochrome P450 genes (Torra et al. 2021). A recent study in Tunisia demonstrated NTSR mechanisms to be involved in metabolic enhancement with TSR mechanisms in 6 populations of corn poppy (Chtourou et al. 2024). Unlike ALS herbicide groups, which target a specific protein, synthetic auxins interact with numerous proteins, including from the following families: TIR1 and Auxin F-Box, AUX/IAA protein, AUX1/LAX influx carrier, PIN efflux carrier, and ABCB (LeClere et al. 2018, Todd et al. 2020, Figueiredo et al. 2022) which makes the identification of TSR alleles very difficult (Jugulam et al. 2011). However, NTSR involving reduced translocation, which limits the movement of synthetic auxinic herbicides to their site of action, has been widely reported in several weedy species, including corn poppy (Rey-Caballero et al. 2016, Torra et al. 2017, Chtourou et al. 2024).

The objective of this study is, therefore, to evaluate the current status of corn poppy resistance to ALS inhibiting herbicides and 2,4-D in Moroccan and Tunisian rainfed cereal zones. Over the years, the reduced number of active ingredients available, as well as the generic threats, add a selection pressure for herbicide resistance already present in several weed species in this geography. For that reason, it is crucial to study and elucidate the occurrence of resistance in order to prevent the increase and spread of herbicide resistance in weeds.

## MATERIAL AND METHODS

Samples were collected at three and five fields randomly distributed across northern zones of Morocco and Tunisia, respectively, based simply on the visual presence of corn poppy previously sprayed with herbicides against broadleaf weeds. For this, sampling of mature seed capsules was carried out across the entire field, ensuring that it was sufficiently representative regarding the genetic diversity of the seed samples. An additional common population of corn poppy was taken from the Atlas Mountains that stretch over 2 500 km from Morocco to Tunisia as a susceptible biotype with no herbicide history (35.0391N, 0.2909E). For each population, seeds were sown directly in plastic pots (diameter: 50 mm, height: 50 mm), placed in the greenhouse located at the Czech University of Life Sciences Prague (49.0915833N, 14.7343022E) and controlled under the same conditions as described by El-Mastouri et al. (2024). In the first experiment, a piece of leaf was taken twice from 50 different plants already sown at the 6-leaf stage. The dried leaves were sent to INRAE (Dijon, France) for analysis using Illumina sequencing in order to detect mutant ALS alleles conferring resistance. The DNA pooled from 50-leaf batches was extracted and diluted (1/10) to perform PCR as described by Délye et al. (2020). Three regions of the ALS gene were amplified separately from each DNA extract with the primer pairs previously designed. These regions carried the eight codons involved in TSR to ALS inhibitors (codons 122, 197, 205, 376, 377, 574, 653 and 654, as standardised after Arabidopsis ALS sequence) 8 and seven additional codons potentially involved in TSR (codons 121, 124, 196, 199, 375, 571 and 578) were included in this genetic diagnosis.

In the second experiment, three new pots per population were sown and treated with four commonly used herbicides in this region (Table 1) at 6 leaf stage. Each herbicide was applied at half of the field rate (N/2), locally registered field rate (N), as well as at double field rate (2N). The trial was arranged in a randomised complete block design with four replications. Efficacy was assessed visually on a linear scale from 0% to 100%, representing the percentage of weed control, 28 days after treatment (DAT). In addition, the number of surviving or dead plants was recorded, and the percentage frequency was calculated. Phenotype scoring was performed as described by Moss et al. (1999). The experiment was repeated twice.

## RESULTS AND DISCUSSION

The phenotypic results indicate varying levels of resistance to both ALS and auxinic herbicides in different populations studied. The majority of populations were considered to be resistant with

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Table 1. Acetolactate synthase (ALS) and auxinic herbicide active ingredients (a.i.) and rates used for each corn poppy population

| Local trade name | HRAC group | Mode of action | Class name | Active ingredient | g a.i./L or g a.i./kg | Local registered rate per ha |
|---|---|---|---|---|---|---|
| Granstar | 2 | inhibition of ALS | sulfonylureas | tribenuron-methyl | 750 g a.i./kg | 12.5 g |
| El Ghoul | 4 | synthetic auxin | phenoxy-carboxylates | 2,4-D-dimethyl-ammonium | 600 g a.i./L | 0.25 L |
| EF-1343[1] | 2 | inhibition of ALS | triazolopyrimidine | florasulam | 50 g a.i./L | 0.1 L[2] |
| Mustang SE | 4 + 2 | synthetic auxin + inhibition of ALS | phenoxy-carboxylates + triazolopyrimidine | 2,4-D-ethylhexyl + florasulam | 300 g a.i./L + 6.25 a.i./L | 0.6 L |

[1]Coded name (product not registered in both Morocco and Tunisia); [2]According to the maximum rate of the active ingredient authorised locally

30% as minimum frequency recorded, which probably indicates limited field efficacies for some of the ALS and auxinic inhibiting herbicides.

Among 8 populations of corn poppy studied (3 from Morocco and 5 from Tunisia), 7 revealed high frequencies of plants resistant to the four herbicides tested at both field and double field rates. Only one population (PAPRH-08) had relatively low but not zero frequencies of resistant plants (less than 30%). All the populations tested for 3 rates of tribenuron-methyl had at least 5 plants resistant at both field and doubled dose (Figure 1) which confirmed very high frequencies of resistance to tribenuron-methyl in both Morocco and Tunisia (Figure 2). These high frequencies (> 75%) were confirmed in all populations located in central Morocco and North-East Tunisia. Five populations of eight had shown high resistance to both half and field rate of florasulam applied solo (Figure 1) and lower survivors at a doubled field rate. However, PAPRH-06, PAPRH-07 and PAPRH-08 were relatively less resistant to florasulam (25–50%) with better control at the highest dose (twice the maximum dose authorised in the field).

The mixture of 2,4-D and florasulam exhibited lower resistance, with fewer survivors and reduced resistance frequencies in the corn poppy populations from both Morocco and Tunisia (less than 25%)-except for PAPRH-03, where nearly 24.15% of the plants were resistant to the mixture when applied at the field rate (Figure 2).

The resistance to 2,4-D was much lower than that to ALS inhibitors. In fact, the doubled field rate of 2,4-D solo in a mixture with florasulam is showing better control (less frequencies of resistance) in both, Moroccan and Tunisian populations. However, it remains moderately strong at field rate and, more specifically, with 2,4-D applied solo (Figures 1 and 2). Among the eight populations tested for resistance to both 2,4-D and ALS-inhibiting herbicides, all the populations had ALS mutant alleles at frequencies ranging from 1.4% to 63.3% (Table 3), and 7 mutations at codon Pro197 were identified. The Pro197 codon was revealed by two and more different mutant alleles: Thr197, Ala197, Ser197, His197, Arg197 and Leu197. No mutations were detected at both Trp574 and Ala122. The codons Thr197, Ser197, Arg197 were most widespread and frequent as they were observed in seven out of eight populations, just ahead of the His197 allele, which was observed in six populations. Leu197 was observed in four populations with the highest frequency in PAPRH-08 (51%). In contrast, Ala197 was detected in two populations only, located in Morocco and Tunisia (Table 3).

High-throughput sequencing of samples from eight fields confirmed the presence of corn poppy populations resistant to ALS inhibitors in both North African countries. These findings align with the results of a recent study conducted in Tunisia (Chtourou et al. 2024). In addition, the data revealed that the alleles carrying a mutation in Pro197 codon are the most frequent, which was confirmed by several studies (Rey-Caballero et al. 2017, Kati et al. 2019, Koreki et al. 2023, Stankiewicz-Kosyl et al. 2023). These alleles confer high resistance to sulfonylurea herbicides, and variable resistance to imidazolinone or triazolopyrimidine herbicides (Duran-Prado 2004, Délye et al. 2011, Tranel et al. 2024) aligning with our phenotypic and genotypic findings regarding resistance levels to tribenuron-methyl and florasulam in both Morocco and Tunisia.

Regarding the auxinic herbicides and more particularly 2,4-D, the selection pressure was extremely

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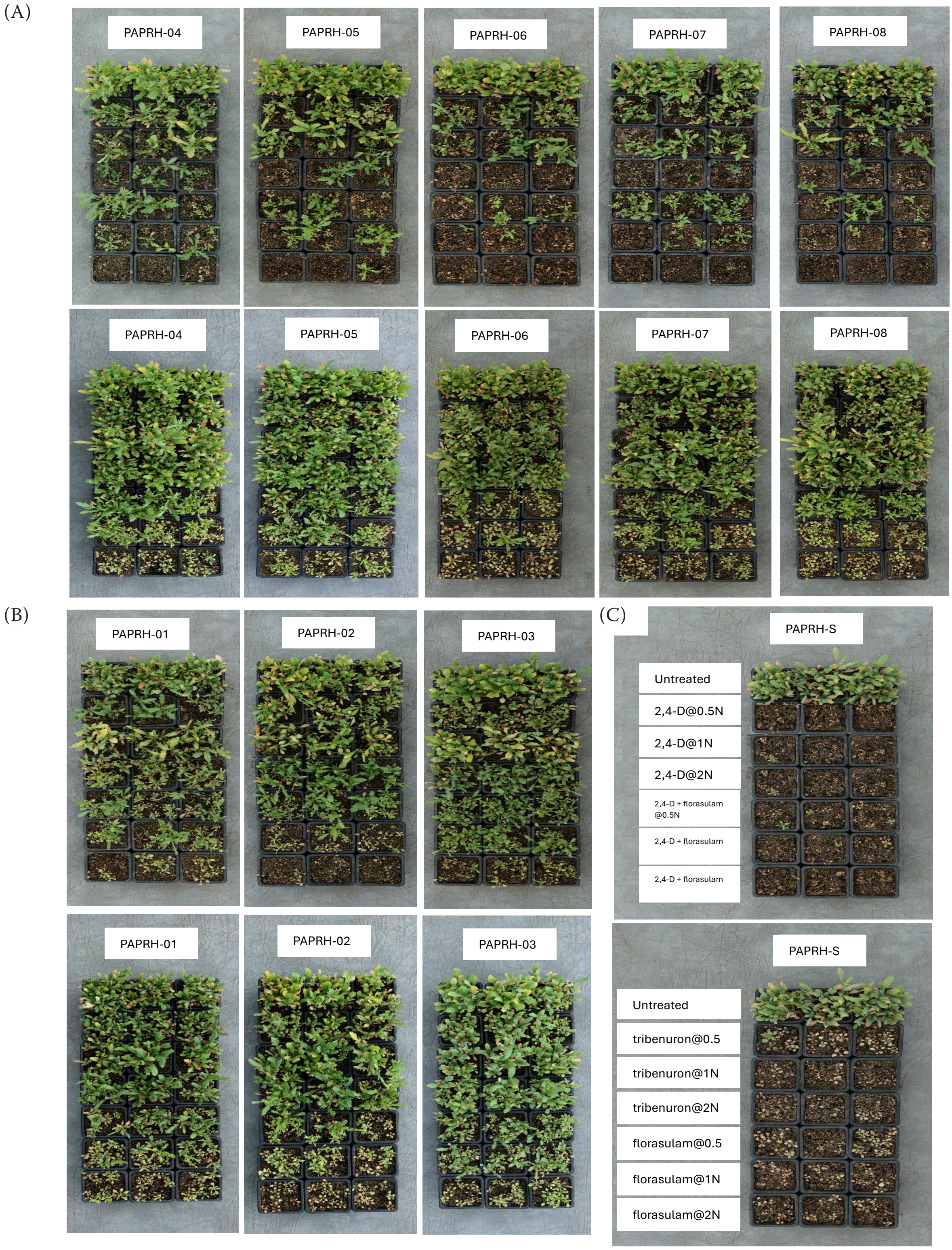


Figure 1. Corn poppy bioassay shows a high frequency of resistant plants. Each image displays untreated control and two herbicide dose-response applications from top to bottom (see section C). A, B – phenotype results of poppy populations from Tunisia and Morocco, respectively; C – phenotype results of sensitive poppy population (PAPRH-S). The top row of each subplot corresponds to the herbicides shown in the upper image of panel C, while the bottom row represents the herbicides displayed in the lower image of panel C, with "N" indicating the highest dose authorised for field application

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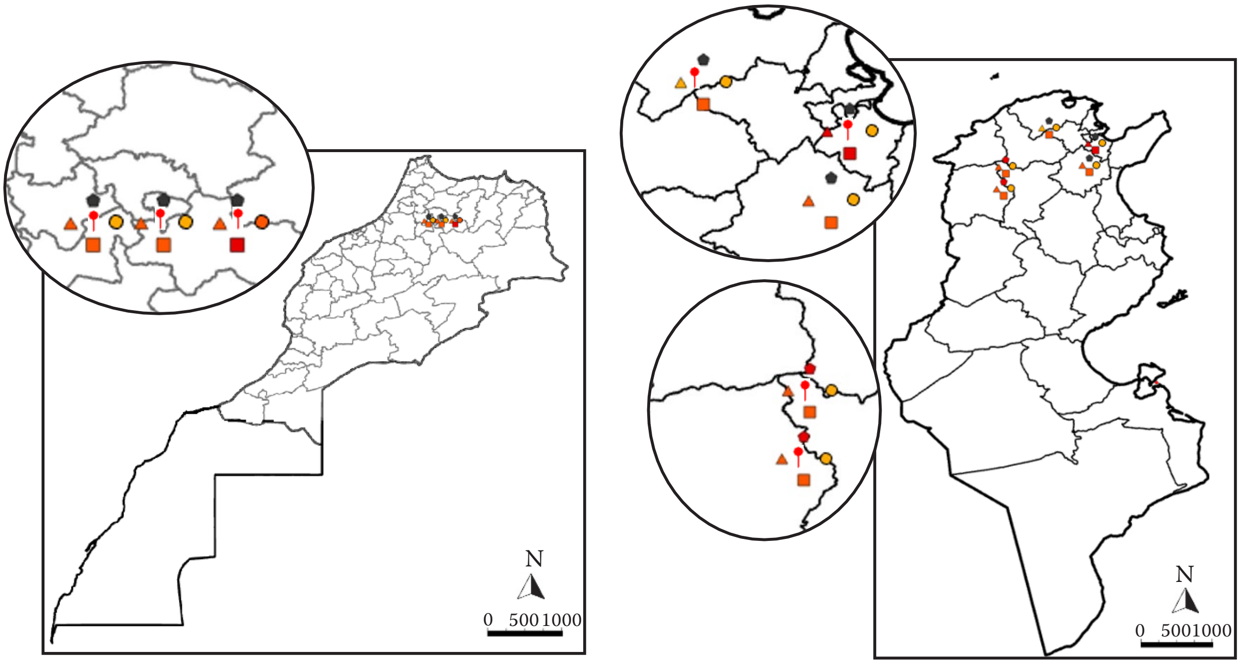


Figure 2. Frequencies of corn poppy plants resistant to acetolactate synthase (ALS) inhibiting and/or 2,4-D herbicides in Morocco (left) and Tunisia (right). Geographical distribution of corn poppy resistant populations to four herbicides: tribenuron (pentagon), florasulam (square), 2,4-D (triangle), and 2,4-D + florasulam (circle) at 5–24% (orange colour), 25–49% (dark orange), 50–74% (red colour), and plus 75% (dark colour). The pin marker in red indicates the exact location of each corn poppy sampled

strong during the 80–90s in Morocco and Tunisia. The first cases of resistance to 2,4-D were accidently observed and confirmed recently (Menchari et al. 2016, Bouhache 2020, Chtourou et al. 2024). Further studies on auxin herbicides are needed in order to elucidate target genes and not rely only on the herbicide sensitivity whole plant assays, by collecting mature seeds from the field, the only way to confirm resistance.

Although resistance to 2,4-D is far from emerging, the selection pressure on auxinic herbicides remains quite low. Nevertheless, the development and emergence of cross-resistance with other auxin herbicides, such as aminopyralid (already reported by farmers due to a decrease in efficacy) or halauxifen, can become potentially problematic in the North African region. More studies in auxin herbicides should be taken into consideration in order to understand and identify resistance mechanisms.

In this research, the study of resistance to ALS inhibitors and 2,4-D simultaneously demonstrated the existence of multiple resistance in *P. rhoeas* populations randomly collected. This situation resulted from the fact that producers generally rely on a single mode of action to control corn poppy, in particular ALS inhibitors. The emergence of resistance to ALS inhibitors resulted in farmers switching to another mode of action, thereby selecting plants resistant to both herbicide classes. Weed management based only on chemical herbicides is not viable in the medium term. However, the use of mixtures reduces rather than delays resistance (as demonstrated with 2,4-D + florasulam mixture). This study also highlights that a full knowledge of the genetic basis for resistance and cross-resistance patterns to ALS inhibiting herbicides could help in designing better chemical programmes adapted locally. A successful integrated management strategy of multiple herbicide-resistant corn poppy populations is necessary to reduce herbicide selection pressure and slow down the increase of new resistant biotypes in these areas.

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Table 2. Overview of the resistance rate by population

| Herbicide rate | Frequency of resistance (%) | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | tribenuron-methyl | florasulam | 2,4-D | 2,4-D + florasulam | tribenuron-methyl | florasulam | 2,4-D | 2,4-D + florasulam |
| | **PAPRH-01**[1] | | | | **PAPRH-05**[2] | | | |
| N/2 | 79.31 ± 0.96 | 44.01 ± 3.21 | 49.53 ± 0.72 | 15.56 ± 1.03 | 81.67 ± 1.60 | 53.34 ± 3.16 | 42.01 ± 2.03 | 12.34 ± 0.90 |
| N | 68.31 ± 1.95 | 20.34 ± 1.14 | 46.68 ± 2.32 | 13.35 ± 1.59 | 80.15 ± 1.19 | 41.02 ± 2.65 | 33.35 ± 3.67 | 13.61 ± 3.28 |
| 2N | 54.03 ± 0.93 | 12.35 ± 8.72 | 34.55 ± 3.89 | 11.31 ± 4.98 | 73.35 ± 5.22 | 22.65 ± 8.11 | 11.67 ± 0.99 | 0.65 ± 4.36 |
| | **PAPRH-02**[1] | | | | **PAPRH-06**[2] | | | |
| N/2 | 83.35 ± 0.96 | 41.2 ± 3.75 | 47.65 ± 0.97 | 34.32 ± 3.79 | 71.67 ± 2.43 | 38.35 ± 3.78 | 41.32 ± 0.92 | 10.34 ± 0.52 |
| N | 81.01 ± 2.25 | 15.34 ± 1.44 | 44.67 ± 0.91 | 10.01 ± 1.26 | 73.11 ± 2.08 | 22.34 ± 1.87 | 32.65 ± 4.35 | 7.68 ± 0.99 |
| 2N | 68.34 ± 3.44 | 5.67 ± 10.04 | 38.61 ± 1.16 | 1.55 ± 7.77 | 69.31 ± 3.71 | 10.13 ± 8.84 | 1.35 ± 1.56 | 0.00 ± 0.00 |
| | **PAPRH-03**[1] | | | | **PAPRH-07**[2] | | | |
| N/2 | 83.11 ± 0.92 | 61.63 ± 2.63 | 46.68 ± 1.18 | 33.51 ± 1.09 | 73.11 ± 1.19 | 44.02 ± 3.30 | 36.68 ± 0.92 | 22.35 ± 2.16 |
| N | 81.34 ± 1.02 | 45.02 ± 5.22 | 44.01 ± 1.40 | 24.15 ± 1.66 | 68.34 ± 1.19 | 29.11 ± 3.11 | 29.01 ± 3.71 | 6.01 ± 1.13 |
| 2N | 75.02 ± 3.51 | 16.34 ± 8.42 | 36.04 ± 1.57 | 10.45 ± 6.99 | 61.66 ± 3.07 | 12.01 ± 9.12 | 2.65 ± 2.46 | 0.35 ± 0.31 |
| | **PAPRH-04**[2] | | | | **PAPRH-08**[2] | | | |
| N/2 | 93.20 ± 0.96 | 68.34 ± 6.66 | 54.01 ± 0.79 | 20.55 ± 3.00 | 77.51 ± 2.56 | 49.34 ± 3.18 | 21.04 ± 1.00 | 13.55 ± 2.48 |
| N | 89.33 ± 1.44 | 41.01 ± 7.32 | 51.63 ± 4.03 | 12.31 ± 1.49 | 73.10 ± 0.64 | 25.01 ± 2.48 | 19.11 ± 2.49 | 1.55 ± 0.46 |
| 2N | 78.35 ± 2.99 | 13.35 ± 10.59 | 24.55 ± 1.53 | 1.01 ± 0.33 | 71.54 ± 6.60 | 7.55 ± 9.19 | 6.68 ± 1.35 | 0.00 ± 0.00 |

[1]Moroccan populations; [2]Tunisian populations

Table 3. Frequency of mutations (%) of the acetolactate synthase (ALS) in percent in *Papaver rhoeas* samples from Morocco and Tunisia

| Population code | Location | GCA | CCT | | | | | | TGG | % total mutants |
|---|---|---|---|---|---|---|---|---|---|---|
| | | Ala122 | Pro197 | | | | | | Trp574 | |
| | | ACA | ACT | GCT | TCT | CAT | CGT | CTT | TTG | |
| | | **Thr122** | **Thr197** | **Ala197** | **Ser197** | **His197** | **Arg197** | **Leu197** | **Leu574** | |
| PAPRH-01 | Morocco – Sais | | 1.7 | | 49.8 | 10.4 | 3.0 | 3.6 | | 68.5 |
| PAPRH-02 | | | 22.8 | | | 15.9 | | | | 38.8 |
| PAPRH-03 | | | 59.2 | 13.7 | 8.6 | | 5.3 | | | 86.8 |
| PAPRH-04 | Tunisia – Ben Arous | | 63.3 | | 1.4 | 6.5 | 4.6 | 7.8 | | 83.6 |
| PAPRH-05 | | | 32.1 | 3.6 | 21.1 | 4.0 | 9.1 | 7.7 | | 77.6 |
| PAPRH-06 | Tunisia – Zaghouan | | | | 12.3 | 12.3 | 33.2 | | | 57.8 |
| PAPRH-07 | Tunisia – Siliana | | 28.8 | | 14.7 | 4.7 | 27.3 | | | 75.5 |
| PAPRH-08 | Tunisia – Beja | | 7.3 | | 1.5 | | 2.6 | 51.0 | | 62.4 |

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