Perspective

Upland Italian Potato Quality—A Perspective

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Abstract: Upland potatoes satisfies consumer demand for high quality foods linked to traditional areas of origin and for new specialties and niche products endowed with added nutritional value, as it is commonly thought that the crop and environment synergy improves the potential beneficial properties of the tuber and gives it a special taste and a renowned quality. Herein, we report considerations on Italian germplasm and the effect of altitude on the sensorial and nutritional value of potato tubers, and investigate the possibility of addressing the nutritional challenge through mountain, eco-friendly, and social agriculture. Finally, we discuss the molecular and biochemical results concerning the impact of altitude on the compositional quality of the tuber, in order to justify promotional claims.

Keywords: mountain; sustainability; altitude; food; health

1. From Andean Potato to Italian Local Ecotypes

1.1. A Taste of History

The potato finds its center of origin in South America, around Lake Titicaca (partly in Peru and partly in Bolivia), where the indigenous people (Quechua) have been consuming this traditional food for about 8000 years. The Inca Empire would dry tubers (chuño) to store or to exchange for goods, which would forever affect the Andean culture and religion [1]. Even today, Peru and Bolivia have an annual consumption of 70–80 kg per person (fresh and processed) and host the largest biodiversity in the world [2]. From the 17th century, the potato spread to the European continent, where, without any doubt, it played an important role in mountain economy [3]. From the Alps to the Southern Apennines, the potato became a major staple food for more than three centuries, during which agronomic practice and selection created many locally-adapted genotypes. When urbanization and the Industrial Revolution caused mass emigration from mountain communities toward the city, the intensive plain agriculture, based on monoculture, replaced upland potato production, marking the decline of its fragile economies. [3]. Fortunately, however, many old local varieties and traditional knowhow did not disappear forever and are still present in the Italian territory, as showed in Figure 1 [4]. Currently, the modern varieties show a reduction in structure genetics caused by the domestication of selective breeding [5]. Thus, the interest of the scientific community towards future global germplasm enhancement, along with changing food lifestyles increasingly sensitive to the geographical area of origin, have stimulated a return to the great biological diversity of the potato, which has a precious source of unexplored quality traits such as biotic resistances and adaptability to a wide spectrum of environments [6].

GENOTYPE
Fiocco di Neve
Turchesa
Viola Germano
Viola Royale (Viola Calabrese)
Biancona di Castelcivita
Postiglione
Tonda Bianca
Ricciona di Napoli
Cannellina Nera
Quarantina Bianca Genovese
Quarantina Prugnona
Formazza
Piatlina
Walser
Bianca del Sindaco
Rossa del Dottore
Vitelotte Malva-Arnaldi
Crispa di Gavoi
Sa Patata 'E Moru
Castagno d'Andrea
Estatina
Rossa di Cetica
Rossa di Sulcina
Cinquantina Vicentina
Formazza
Lunganna
Roti Ojgie

Figure 1. Italian local varieties—(**a**) "Ricciona di Napoli" field in flower; (**b**) "Fiocco di Neve" plant in flower; (**c**) "Ricciona di Napoli" tubers; (**d**) "Patata 'E Moru" tuber; (**e**) "Rossa di Cetica" tubers; (**f**) "Viola Calabrese" tubers. The different colors of the list indicate the regions of origin. Source: Mandolino et al., 2015 [4].

1.2. Traditional Italian Varieties

Over the last fifty years, the cultivation of traditional ecotypes and well-known, popular cultivars have overlapped within the same areas and, despite these traditional local varieties having different names, they are sometimes in fact genetically identical to the cultivars. A surprising comparative study was recently carried out on 28 ecotypes, with a total of 54 accessions recovered in eight different Italian regions, and between over 2000 varieties belonging to EU Common Catalogue and to the SASA variety collection [4]. The outcomes of such fingerprinting carried out by twelve SSR (microsatellites or single sequence repeat) markers, allowed for highlighting the genetic similarity, for example, of "Castagno d'Andrea" (from Tuscany) to cv. Kennebec, an American white-fleshed, mid-late variety, and similarly

"Rossa del Dottore" (from Piemonte) to cv. Desiree, a Dutch red-skinned and yellow-fleshed variety. Moreover, an example is "Malva Arnaldi" (from Piemonte), which resulted in being genetically identical to cv. Vitelotte Noir, a traditional purple-fleshed potato whose color is conferred from the anthocyanins—phenols appreciated for their well-known health properties [7]. A careful fingerprinting is thus necessary to guarantee the genetic distinctiveness of traditional local potatoes. Recently, "Ricciona di Napoli" (from Campania) has represented an excellent example of an ecotype that did not show a genetic profile similar to any other genotype [4]. Its well-established historical and geographical identity, its traditional use by farmers, cultural fondness of consumers, and good agronomic and organoleptic characteristics were the main reasons for its rediscovery (project «Pat.Ri.Na.»—"Progetto di valorizzazione della patata Ricciona di Napoli", funded by the Campania Region and coordinated by OP Campania Patate; Figure 2) [8]. Nevertheless, had it not shown a unique genetic profile, it would not have been reintroduced to the market properly. Many local genotypes find their typical and traditional areas of cultivation in the Italian mountains, but it is necessary to distinguish them unambiguously from the most commonly used varieties, such as cv. Kennebec, cv. Vitellotte, and cv. Desiree, in order to promote them properly.

Figure 2. Packaging of cv. "Ricciona".

1.3. Today's Mountain Potato

Beyond the genetic features, the traditional, local, and rural farming, often typical of mountain families [3], perfectly matches a renewed consumer interest in territoriality, generally perceived as a guarantee of healthier and safer food for humans and the environment, and in contrast with the world-wide, urban, fast, and cheap identity, typical of the extensive plain cultivation. Of all of the major crops, the potato is arguably one of the most important species sustaining the mountain family farming [3]. Nevertheless, many factors penalize small-hold farmers in mountain areas who struggle to compete with large-scale producers from the lowlands, and potato production in Italy remains concentrated in flat areas. The main reasons are the productive performance of upland ecotypes, which are decidedly lower than plain cultivars, and the negative influence of the mountain environment on the tuber yield [9]. It is also true that plain and mountain potatoes do not share the same harvest time, which makes the late summer–autumn harvest of the latter potentially profitable. But, it is for the same reason, Italian mountain potatoes compete with the cheaper ones from North Europe. The result is an elite product whose target consumer is a high-end spender. However, its price, albeit higher, reflects tradition and territory, and many elements have to be considered to contribute to its full potential and economic value, namely: quality; awareness of sustainable and organic farming;

and the combination of economic, cultural, and social factors. Its promotion should also be seen to provide local smallholders an opportunity to increase profits, and should represent a source of employment and mountain depopulation alleviation. Low-income family farming is poorly integrated in the commodity market, and specific policy interventions could represent an opportunity to receive greater support. Along with the debate as to whether upland potato farming should be sustained, in 2018, European politics have moved towards the labelling of mountain products, as the Italian denomination "Prodotto di Montagna" [10], which should guarantee premium prices. Similarly to the protected denomination of origin (PDO) ("Patata di Bologna") and the protected geographical indication (PGI) ("Patata della Sila"), but with fewer procedures and costs, this new provenience certification scheme was created to sustain the traditional linkage between the environment and quality, and communicating to consumers that the geographical area influences the final composition of the product [11]. Is this however true? The environment may greatly influence the overall biochemical and nutritional status of tubers, with consequent effects on human diet [12,13], but little or no information is available concerning tuber response to local provenience and its putative surplus value for justifying claims to mountain denominations, and protecting consumers from the possible exploitation of their trust in upland potato quality.

2. Influence of Upland Farming on Potato Quality

"Mountain potato" is a catchy term, and its increasing popularity with the consumer is influencing its true market power. Overall, European consumers recognize high quality in mountain products [14]. Here, we give an overview of how altitude impacts the organoleptic characteristics and the content of components with potentially health-promoting effects, especially the antioxidant contents generated as a response to reactive oxygen species in plants.

2.1. Nutritional Properties

The nutritional contribution of potato tubers to the human diet is mainly due to carbohydrates (c.ca 20%); proteins of fairly high quality, with an amino-acid pattern well matched to human requirements (2%); lipids (0.1%); and organic acids (0.4%–1%) [15]. A single medium-sized potato contains about half the recommended daily intake of vitamin C (20 mg/g d.w) [16] and a fifth of the recommended daily value of potassium [17]. However, in the past, interest has been focused greatly on secondary plant metabolites, such as phenols (0.2 to 219 mg/g DW) [18], flavonoids (0 to 45 mg/g DW) [17], and carotenoids (1.10 to 12.2 mg/kg DW) [19], due to their antioxidant activity conferring protection against degenerative and age-related diseases [18]. Anthocyanins, the major plants flavonoids, are the main pigments responsible for the red-blue color of many crops [7], such as potatoes, which are only present in colored tubers. Red potatoes have acylated glucosides of pelargonidin, whereas purple potatoes, such as cv. "Vitelotte", also have acylated glucosides of malvidin. Anthocyanins confer health benefits in the human diet as antimutagen, anticarcinogen, and antiglycaemic agents, through a hydrophilic antioxidant activity comparable to those provided by Brussel sprouts or spinach [7]. Their physiological role in the epidermal tissues of plant organs is to protect the underlying tissues from UV radiation damage, strongly affecting the photo-biological metabolism related to protection and their repair mechanisms [20]. Therefore, flavonoids and phenolics are named "UV-absorbing compounds" (UVACs) [21,22]. As many other factors contribute to the complexity of the mountain ecosystem, solar UV-B radiation depends, to a large extent, on altitude [23]. As elevation increases, the air mass decreases, which links to greater atmospheric transparency, especially with regards to shorter wavelength radiation as in the UV-B range (280–315 nm) [24]. UV-B enhances the accumulation of flavonoids and related phenolics [20–22], probably triggered by genes that encode phenylalanine ammonia lyase (PAL) and chalcone synthase (CHS) [25,26], which has a strict light requirement to be expressed in *Arabidopsis thaliana* [27]. CHS is induced in response to UV-B, by means of a signaling pathway model that passes through the UVR8 regulation (UV-B receptor UV resistance locus 8a) [28]. Anthocyanin synthesis is controlled by three loci, *D*, *P*, and *R*,

which have been localized to chromosomes 11, 2, and 10, respectively [26]. *P* and *R* were found to be the genes encoding the biosynthetic enzymes involved in purple anthocyanin synthesis flavonoid 3′,5′-hydroxylase (F3′5′H) and dihydroflavonol 4-reductase (DFR), whereas *D* encodes an R2R3 MYB named StAN1, which is similar to petunia AN2 [29–32]. StAN1 is the key regulator of anthocyanin biosynthesis in the coloration of potatoes and is modulated by sucrose [33], whereas its involvement in the response to environmental factors such as UV-B has not yet been shown. Unfortunately, most studies are focused on the above-ground plant parts, such as the leaves [34]. What is less clear, but more interesting, is the effect of light on the subterranean organ, as the dietary value of the potato is a tuber. In the roots of *Gynura bicolor*, for example, anthocyanins only accumulate when directly exposed to light [35], whilst an indirect effect of light on the tuber was suggested. Indeed, increasing the phenolic content was observed in the tubers grown at increased elevation sites (1141 m and 2010 m a.s.l) [9]. Even though the long transport of anthocyanins from source to sink has never been demonstrated, it has been convincingly shown that their precursors (e.g., naringenin) can be transported from shoots to roots, where all of the enzymes required to complete their biosynthesis may be present [36]. It is therefore possible that the anthocyanin precursors, rather than anthocyanins per se, are synthesized in the shoot, and then transported to the organs that grow in the dark. Additionally, it has recently been hypothesized that some GSTs are also involved in this long-distance transport system [37]. Nevertheless, the mechanisms of anthocyanin transport remain poorly understood, as does its response to UV radiations, and they warrant further investigation. However, UV-B radiation is not the only highland factor influencing the biochemical changes in tuber composition. In accordance, imposing UV-B treatment at +20% compared to the UV-B level observed at the upper experimental site, the increase of phenolics in the artificial experiment was −38% than the natural field [9]. Other factors, therefore, must be influential on the phenolic content. Besides protecting against UV radiation, anthocyanins also respond to cold temperatures, probably in association with DFR gene activation [38,39]. Indeed, purple- and red-fleshed potatoes grown at northern latitudes showed higher anthocyanins and total phenolic content (2.5 and 1.4 times, respectively) [40], probably in response to an induction of expression of the hydroxycinnamoyl-CoA quinate hydroxycinnamoyl transferase (HQT) and cinnamate-4-hydroxylase (C4H), key enzymes for phenol biosynthesis in potato tubers [33].

Based on the above discussion, can differences in the secondary metabolites be considered sufficient to affect the nutritional quality of the upland potato? In contrast to common belief, the potato is one of the richest sources of phytonutrients in the world in diets. Indeed, even though other crops have a higher content of beneficial bio-compounds [41], the potato is one of the most widely consumed [42]. Therefore, even modest changes in tuber composition can cause big changes in human nutritional intake [43], and the significance of altitude on tuber composition can be considered a useful approach to achieving the global goal of increasing the availability of nutrients to the consumer. In addition, often mountain farming is organic farming that could itself be considered relevant to diet and health, even though a great debate is currently ongoing, and an objective and exhaustive assessment has not been reached [44,45]. Considering that upland potato cultivation is part of a system that goes beyond the effects of altitude on tubers and embraces a global concept of environmental agroecosystem, we shall consider that in European mountain regions, organic family farms are often the most viable forms of agriculture. A reduction in the environmental impact of agriculture preserves the naturalness of the products. At higher altitudes, fewer phytochemicals are required, because the potato is less challenged by nematodes; insects, such as the potato tuber moth and potato beetle; aphides; and soil-borne viruses. In addition, a more sustainable management of water resources and anti-sprouting agents is possible. Traditional mountain knowhow often leads small farmers to adopt organic practices that have been used locally for decades. Sometimes, for example during the winter, tubers can be stored on Italian slopes in fern-covered holes in the soil, avoiding cold storage chambers or anti-sprouting agents (Figure 3).

Figure 3. August/September tuber storage on the slopes of Etna (Randazzo, CT, 765 m a.s.l; Italy).

2.2. Organoleptic Properties

Moreover, the sensory evaluation of the upland potato is necessary in order to assess its global quality. Even though potato producers usually carry out the panel test to select the most suitable genotypes for cultivation in upland areas, little scientific evidence supports the hypothesis of an influence of highland cultivation on the organoleptic characteristics of the potato. An increase in the amylose/amylopectin ratio was observed in the tubers grown at higher elevations, where high values of amylose impact positively on texture [46]. This observation is consistent with its significant improvement in boiled potato grown at a higher altitude, but studies are still few and fragmentary [47]. A possible explanation is provided by evidence of alterations in the glucan chain length distribution of the starch structure, which is observed in the tubers grown under low temperature conditions [48]. This response could be triggered by the activation of the plastidial phosphorylase 1 and the inhibition of the starch synthase [48]. However, it is currently impossible to draw unequivocal conclusions and further studies should be implemented.

3. Future Perspectives

Biofortification programs aimed at optimizing tuber phytonutrients for disease prevention are ongoing, and not only include molecular breeding for the selection of new genotypes, but also a suitable choice of environment to improve the natural beneficial composition of the plant. This is particularly relevant to the potato. New biofortified genotypes are hard to obtain through conventional selective breeding with wild potato species, often described as particularly rich in beneficial phytonutrients [49]. For example, group Phureja has contributed different traits to modern yellow-fleshed potato cultivars [6]. The presence of incompatibility barriers caused by the genetic complexity of the *Solanum*

genera, characterized by a tetrasomic inheritance and high heterozygosis, could hamper the backcrosses necessary to obtain hybrids [6], unless new plant breeding techniques are adopted (NPBTs) [44].

Mechanisms Underlining Natural Adaptation to Upland Environments

A future perspective could be to investigate the environmentally triggered epigenetic traits that could control the quality features to further identify the stable and hereditable marks for potato quality improvement. Indeed, even though the effects of environmental stimuli on potato transcriptome can explain a wide range of transient changes, the emerging new sources of phenotypic variations could explain the stable changes that persist after stimulus, and underlie the adaptation of potato to different habitats, such as mountain areas. Unfortunately, new technologies have so far been applied to model species such as *Arabidopsis thaliana* [50] and *Zea mays* [51], with evident limitations in transfering knowledge to non-model species, due to specific genomic features and ploidy levels. Nevertheless, Liu et al. [52] have successfully shown that lycopene accumulation during tomato fruit ripening is under epigenetic control, as follows: carotenoid biosynthesis depends on the DEMETER-LIKE DNA Demethylase 2 (DML2) responsible for the DNA methylation level. This example illustrates how epigenetic marks can influence the accumulation of a metabolite that contributes to the quality and the nutritional value of tomatoes. We could speculate on a complex genetic and epigenetic network that could emerge as a source in the explanation of the impact on quality traits of a transgenerational adaptation of potato to upland areas. Indeed, plant adaptation to an environment depends on a complex interaction between genetic variation and phenotypic plasticity. Growing evidence shows that the genetic sequence alone cannot explain the full spectrum of phenotypic diversity and its heritability in plants. The so called "plant memory" could play a role in the fitness of the plants through the heritable and stable modifications not mediated by the changes in the underlying DNA sequence. Epigenomes are remodeled during the plant development and in the response to environmental stimuli, such as drought, salt, temperature, and pathogen/herbivory attacks, generating a hereditable phenotypic variation, classified as cis-acting meQTL and trans-acting meQTL [53]. The former is due to SNPs tagging structural variants such as transposable elements (TE), causing siRNA silencing or spreading DNA methylation into flanking regions of the coding genes. The latter affects the methylation levels at the genome-wide scale, causing changes inside the chromatin control genes, with effects that can be adaptive [54]. Numerous studies have addressed the silencing of TE by DNA methylation as a mechanism of trans-generational memory. The functional relevance that epigenetic mechanisms have on evolutionary adaptation to a specific habitat was shown by Dubin et al. [55]. Using genome wide association studies (GWAS), they revealed that CHH methylation increases with temperature and CpG gene body (GBM) methylation with the latitude of origin. The consequence is that chromatin could mark local adaptation, contributing to plant phenotypic plasticity. Chromomethylase 2 (CMT-2) is supposed to be an adaptive locus, whose role is the genetic controller of plant temperature tolerance through the regulation of epigenetic modifications in natural adaptation [56,57]. Similarly, Rius et al. [51] identified in maize a crosslink between a quality trait, such as the content of flavonoids, and an epigenetic regulation mediated by the altitude and the level of UV-B. The DNA methylation in the promotor, intron 1 and intron 2 of P1, a R2R3-MYB transcription factor that regulates the accumulation of flavonoids, is lower in the landaraces of maize adapted to a high altitude than in a low altitude inbred line, probably caused directly by an adaptation to UV-B radiations. Indeed, UV-B radiations can change the chromatin structure of plants [58], showing how plant adaptation to contrasting environments could evolve in different epigenomes. Beside the importance of the epigenetic mechanism underlining the plant adaptation to environment, a great debate on a possible restoration of epigenome changes through reverse epimutation put at risk the basis upon which transgenerational stress memory is built, because an environmental induced epigenetic status could be reset [50].

To date, few studies have focused on the epigenetics of the potato. Recently the miniature inverted-repeat transposable elements (MITEs) involvement in the fine regulation of the potato tuber

skin color (Class II, MITE F3′5′H) [59] has been identified. Their insertion within the first exon of the gene encoding for F3′5′H, causes its inactivation. However, the possibility of a "transgenerational stress memory" to explain long-term upland potato adaptation has not so far been addressed. Interestingly, Ibanez [9] reported that natural populations of wild potato species *S. kurtianum* that have already adapted to different altitudes showed a different increase in UVAC when exposed to +UV-B treatments, and epigenetic regulation of altitude mediated by the effect of UV-B radiation cannot be excluded, as previously shown in maize [51]. A future direction could be the effective exploitation of epigenetic-based phenotypic diversity of potatoes traditionally grown and produced in mountain areas in shaping quality traits, and the identification of adaptive loci associated with different altitudes in genotypes of *Solanum tuberosum* grown and adapted to different habitats and their potential use for plant improvement.

4. Conclusions

In conclusion, the paper aims to stimulate fresh thinking on the close link between the Italian mountain areas and the traditional local varieties of potato, and investigate the effects of altitude on the nutritional quality of potato tubers, together with the environmental and social implications. The molecular features underlining the potato adaptation to upland environments and the corresponding biological processes involved are also discussed.

It is important to point out the predominance of genetics over environmental effects when explaining the variations of biochemical tuber composition, in order to support the importance of the genetic distinctiveness of the ecotypes. However, our view is to treat this crop as part of a system that extends beyond the genetic features, to create a connection with the environmental ecosystem. Whether and in which ways altitude really affects the organoleptic and nutritional value of tubers has not been clarified exhaustively, and supplementary information to both consumers and producers is necessary. Nonetheless, the variation in metabolites observed in response to collective environmental influences raises questions about the extent to which these pathways can be stimulated by environmental inputs in a manner that enriches nutrients for health improvement while, at the same time, protecting yields [33]. Many studies are focused on the response to UV, documenting its importance above the other environmental factors that compose the complex upland system. However, it is necessary to extent these studies to what actually happens in the real-world, and future efforts shall approach omic techniques applied to potato grown in experimental gardens at different altitudes. In our context, the magnitude of environmental variations between study sites and the difficulties in showing how altitude can improve tuber health promoting compounds suggest caution, primarily because the nutraceutical value of a food product needs to be accurately demonstrated before adopting promotional health claims, as stated by the European Commission concerted Action on Functional Food Science in Europe (FU.FO.S.E.). The promotion of upland potato farming should also comply with consumer preferences and increasing community resilience in the face of mountain depopulation. Our perspective is to encourage studies that compare plains and mountains, as well as to investigate the molecular mechanisms underlining the natural adaptation of potatoes to upland environments.

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