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Nondormant mutants in a temperate tree species, *Corylus avellana* L.

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Summary. Nondormant mutants in hazelnut (*Corylus avellana* L.) are described. In contrast to normal trees in which physiological rest, or dormancy, is induced by short days, mutants fail to respond to this stimulus. Shoot tips continue to grow, old leaves are retained until midwinter when they are frozen and/or pushed off by developing axillary buds, axillary buds begin to grow in December, 2–3 months before normal spring bud break, and cold hardiness does not develop. Nondormancy is controlled by a single recessive gene (*dd*). The mutation is not uncommon since eight cultivars, including the world's most important commercial cultivars, are heterozygous for this trait. The implications of nondormancy in a temperate tree species are discussed in relation to evolution, extension of the range of cultivation, breeding, and value for basic studies of fundamental mechanisms of dormancy.

Key words: Dormancy – Hazelnut – *Corylus* – Inheritance

Introduction

Dormancy is a prerequisite to cold acclimation in temperate deciduous tree species (Weiser 1970). In autumn, like most other winter-hardy trees, the hazelnut (*Corylus avellana* L.) undergoes the physiological and morphological changes characteristic of dormancy. Terminal shoot growth ceases, shoot tips abscise, leaves abscise, buds develop protective waxy foliar structures (scales and stipules), true winter rest ensues, as evidenced by the existence of a chilling requirement, and cold resistance develops.

Genetic studies of vegetative bud dormancy in temperate tree species have been limited primarily to comparisons between latitudinal and altitudinal differences in length of the critical photoperiod for dormancy induction. Genetic variability in photoperiodic response and photoperiod-temperature interactions have been amply demonstrated (Downs and Bevington 1981; Downs and Piringer 1958; Irgens-Moller 1957; Nitsch 1957; Pauley and Perry 1954; Vaartaja 1959). These differences represent natural selection for dormancy responses that are synchronized with the local climate. Limited inheritance studies made by crossing ecotypes with a short and long critical photoperiod indicated that many genes are involved in the regulation of this response (Pauley and Perry 1954; Perry 1971). Because of the diverse environmental factors that can influence and induce dormancy and the multitude of physiological processes involved, Perry (1971) concluded that "a large number of genes are definitely involved". There are no reports indicating that one or a few genes are responsible for vegetative bud dormancy in trees, but this simple mode of inheritance regulates seed dormancy in some species (Eenink 1981; Garber and Quisenberry 1923; Johnson 1935; Whittington et al. 1970; Shifriss and George 1965).

In the Oregon State University hazelnut breeding populations, nondormant trees have segregated frequently in progenies from certain parental combinations. In this paper the nondormant trait is characterized and evidence is presented for monogenic control. The implications of the discovery of nondormant genotypes of this temperate tree species are discussed in relation to evolution, breeding, potentials for extending the cultivated range of this crop, and studies of the fundamental mechanisms of vegetative bud dormancy.

Materials and methods

General observations were made on dormant and nondormant trees for several years both in the greenhouse and in the field. To obtain more precise information on the response of one- and two-year-old mutant trees to specific winter temperatures, detailed observations were made on a population of 6,236 seedlings which included both normal and mutant genotypes.

One-year-old trees were planted in the field at Corvallis, Oregon, in October, 1982 and evaluated four times: February 5, 1983; December 28, 1983; March 30, 1984; and September 10, 1984. Maximum-minimum temperatures were obtained from a nearby recording station.

The first evaluation consisted of rating the extent of freeze damage to individual trees (none, slight, moderate, severe, or dead). Injury consisted of varying amounts of dead tissue in shoots, swelling buds, and young expanding leaves. At this time, and at the next two evaluations, the stage of axillary bud development was rated on a scale of 1 (no swelling) to 10 (largest leaves 5.5 cm in diameter). At the second evaluation, plants were rated as dead or alive, and observations were made on retention of leaves, presence of a growing shoot tip, and stage of axillary bud development. At the third evaluation, plants were evaluated for freeze damage (none, moderate, severe, or dead), and for stage of bud development. At the fourth evaluation, the amount of regrowth of damaged trees was recorded.

For inheritance studies records were made for eight years on the numbers of nondormant seedlings in all progenies consisting of from 20–425 individuals. A total of 289 parental combinations and 20,322 offspring were evaluated. Although 75 progenies (26% of the total) segregated for nondormancy, chi-square analyses were made for only the 55 families that contained 30 or more individuals. Plants were classified as dormant or nondormant in December–January, when normal trees are dormant. Criteria used were the presence of a shoot tip, leaf retention, and precocious growth of axillary buds. Crosses were made solely to further the breeding objectives and not to generate nor to avoid mutant segregants. While some clones were used as parents in only a few combinations others were used repeatedly, e.g., Casina was used in 37 different combinations, Ennis in 28, Lansing in 23, and Montebello in 18.

Results

General characteristics of nondormant mutants

In nondormant mutants the morphological and physiological processes associated with the onset of dormancy in autumn do not develop. Shoot tips do not abscise, as is characteristic of this species, but continue to grow and form new leaves, albeit very slowly as temperatures become increasingly cooler. If not killed by subfreezing temperatures, old mature leaves do not abscise until midwinter when they senesce and fall, or are pushed off by developing axillary buds. Axillary buds do not form waxy scales and stipules, but begin to grow in December–January. Based on field observations, nondormant trees are considerably less winter-hardy than normal trees. Preliminary artificial freezing tests on detached branches substantiates this reduced hardiness (K.K. Tanino, unpublished results).

In Corvallis, Oregon, in any given season, the extent of precocious winter axillary bud growth and new shoot development depends on the plant's genotype, the autumn and early winter temperature, and the date at which damaging temperatures occur. The most advanced axillary bud development that has been observed occurred in the particularly mild autumn and early winter of 1981–1982. The temperature had dropped to −3 °C only two nights before January 9, 1982, when it reached −9 °C. By this time, in the earliest leafing nondormant trees axillary shootlets had reached 2–4 cm in length, with expanded leaves 2–3 cm wide. The sudden drop in temperature killed all these succulent young tissues although one-year and older wood on most trees survived and regrew later in the spring.

Axillary bud break seems to be somewhat inhibited by the presence of old leaves, but not completely as in normal plants. Although trees have not been hand-defoliated, axillary buds develop more rapidly on parts of stems where leaves senesce and fall earlier. As in normal plants, mutants exhibited a range in time of bud break, some beginning growth considerably earlier than others. In years when nondormant trees were not freeze-damaged, there was a striking contrast in the growth status of normal and mutant trees in the field by mid-February. Normal trees had not yet started to grow whereas nondormant mutants had expanded leaves 4–6 cm wide.

Only limited observations on the reproductive behavior of nondormant mutants have been possible under field conditions in the Willamette Valley of Oregon. Most hazelnut seedlings do not produce flowers until they are four years old. Thus, in order to bloom, the mutants must survive three winters in the field with minimal damage. This situation has occurred once in the past eight years. Many nondormant trees planted in October, 1980, survived three successive winters during which the temperature did not fall below −9 °C. Some of these trees flowered in November–December, 1983. Pistillate flower clusters are in the terminal position of a compound bud, and flowers normally emerge well in advance of leaves. In the nondormant mutants, which typically have precocious bud break, pistillate anthesis occurred considerably earlier (November) than in normal trees (mid-December to February). By contrast, anthesis in staminate flower clusters (catkins), which develop separately from leaf buds, occurred in the early part of the normal range (December–February). Unfortunately, these flowering nondormant trees did not bear nuts because the temperature dropped to −12 °C on December 25, 1983, and all trees were killed or very severely injured.

In the greenhouse, at natural daylengths and favorable temperatures for growth, normal hazelnut seedlings planted in August–September stop growing in late October – early November in response to the shortening daylength. They do not, however, develop typical dormant morphology. Specifically, leaves are retained and shoot tips form a tight cluster of over-

Fig. 1. Normal dormant hazelnut trees and adjacent nondormant mutant trees with leaves and growing shoot tips. Photo taken December 28, 1983

lapping, small leaves rather than abscising. In the greenhouse, normal trees remain in this non-growing condition for several months, and by the next summer only a small percentage of them will have started to grow. Most require a chilling period to resume growth. In contrast, nondormant seedlings continue to grow all winter in the greenhouse, regardless of daylength, although water, nutrient, or pest stress can cause growth to stop. On one occasion, in mid-September a group of three-year-old nondormant seedlings and one-year-old normal grafted trees in the greenhouse were water-stressed sufficiently to stop growth in all trees. When regular watering was resumed the nondormant plants began to grow, and grew continuously for the next 1½ years, while the normal trees dropped their leaves, formed typical dormant buds and remained alive but completely dormant for the next 1½ years. In normal trees the water stress and subsequent short days induced dormancy which would have required chilling temperatures to break.

Specific observations of 1981 seedlings

One-year-old seedlings which had been planted in the field October, 1982, were first evaluated for freeze damage and axillary bud development on February 5, 1983, five weeks after the coldest period of that winter. During a four-day period at the end of December the temperature had dropped to –6 °C. Of 404 nondormant mutant trees, 246 (61%) were rated as undamaged or only slightly to moderately damaged and 158 (39%) were rated as severely damaged. By midsummer the 246 trees with little or no damage were fully recovered and indistinguishable from normal trees. Of severely injured trees, 114 (72%) had recovered and 44 (28%) died. Thus, during the 1982–1983 winter 11% of all nondormant trees were freeze-killed. All normal, dormant trees were undamaged.

The February 5, 1983, rating of axillary bud development of nondormant trees ranged from 2 to 6. Most (96%) normal trees were completely dormant (rated 1), while in a few (4%) buds were barely swelling (rated 2).

In the 1983–1984 winter, the most severe temperatures were –9° to –12 °C on December 21–25, 1983. Three days later, all trees were evaluated for the amount of cold injury and for the stage of axillary bud development. All nondormant mutant trees appeared severely damaged. They had retained most or all of their leaves, and their shoot tips were present and appeared to have been still unfolding new leaves at the time of freeze damage (Fig. 1). In many trees axillary buds had swollen and some had reached stage 5 (largest leaves expanded to 2.5 cm). All normal trees appeared undamaged, and axillary buds were unswollen (rated 1).

To obtain a more accurate evaluation of damage, trees were reevaluated March 30, 1983, at which time buds had begun to swell on the latest developing normal trees. Of the 404 nondormant trees, 341 (84%) appeared dead and the other 63 (16%) were so severely damaged that accurate ratings of bud development could not be made. Axillary bud development ratings for normal trees ranged from 2 to 10 (largest leaves 5.5 cm wide) and there was no evidence of winter damage.

Regrowth of damaged trees was evaluated in September. Of the 341 trees that had appeared dead in

Table 1. Hazelnut clones heterozygous for nondormancy (*Dd*) and homozygous normal (*DD*), and their origin

Genotype			
Dd (48 clones)		*DD* (33 clones)	
Clone	Origin	Clone	Origin
'Barcelona'	Major OR cv. So. France	'Butler'[a]	Minor OR cv. Oregon
'Compton'[a]	OR selection	'Creswell'	Minor OR cv. Oregon
'Lansing'[a]	OR selection	'Daviana'	Minor OR cv. England
'Montebello'	Minor OR cv. Sicily (?)	'Ennis'[a]	Minor OR cv. Oregon
'Negret'	Major Sp. cv. So. Spain	'Gasaway'	Minor OR cv. Oregon
'Pearcy 14'[a]	OR selction	'Hall's Giant'	Minor cv. Germany
'Riccia di Talanico'	Impt. Ital. cv. Italy	'Henn. # 3'	Unknown Eur. orig.
'Tombul'	Major Turk. cv. Turkey	'Jemtegaard 5'[a]	Minor OR cv. Oregon
'Tombul Ghiaghli'	Greek cv. Turkey	'Neue Riesen'	Minor Eur. cv. Germany
'T. G. Delle Langhe'	Impt. Ital. cv. No. Italy	'Casina'	Minor Sp. cv. No. Spain
'Tonda Romana'	Impt. Ital. cv. Italy	23 seedlings	OR breeding prog.
25 'Barc.' sdlgs.	OR selections		
5 'Montebello' sdlgs.	OR selections		
4 'T.G.D.L.' sdlgs.	OR selections		
3 uncertain origin			

[a] Probably open-pollinated Barcelona seedlings

March, 69 (20%) had some regrowth from basal suckers or from older, lower parts of the young trees. Of the 63 that had been rated as severely injured 61 regrew. The extent of regrowth varied from few very weak shoots to many strong shoots.

There were differences in hardiness among the nondormant mutants. After two winters in the field 68% of the nondormant trees were dead. Eleven percent were killed during the winter of 1982–1983 when the minimum temperature was −6 °C, and an additional 57% died during 1983–1984 when the temperatures dropped to −12 °C. The 32% of nondormant trees which were severely damaged, but survived, had varying amounts of regrowth.

Inheritance of the nondormant trait

Segregation for the nondormant trait has been repeatedly observed during the past eight years. Chi-square analyses were made to test the hypothesis of a 3 : 1 ratio because it appeared that approximately 25% of the trees in segregating progenies were nondormant. A total of 4,010 seedlings were evaluated from 55 segregating progenies, each consisting of 30 to 352 individuals. For 51 of these progenies the chi-square value ranged from 0.003 to 3.60 ($P = 0.05$ to over 0.95) and for four of them the chi-square ranged from 5.17 to 6.30 ($P = 0.01$ to 0.05). The evidence strongly supports the hypothesis that the nondormant trait is determined by a single recessive gene (*dd*).

Because of the high frequency of heterozygosity for the nondormant gene in desirable clones, the repeated use of some of these clones in different parental combinations, and the large number of crosses made, segregation for this trait occurred so frequently that it has been possible to verify the genotypes (*DD* or *Dd*) for 81 clones (Table 1). Of the 48 clones which are heterozygous (*Dd*) 11 are named cultivars, including 8 which are among the commercially most important in the world, and 37 are seedlings derived from these eight commercial cultivars. Thirty-three clones are homozygous normal because when they are crossed to known heterozygotes nondormant offspring do not appear. The *DD* genotypes included 10 named clones, none of which are important cultivars, and 23 seedlings from the breeding program.

Discussion

The discovery that the most important commercial cultivars from all major growing regions are heterozygous for the nondormant gene indicates that this mutant occurs frequently and over a wide geographic region. Three lines of evidence suggest that the mutant has arisen independently, at least in most of the eight commercial cultivars. First, the cultivars originated in widely diverse geographic regions – Turkey; northern, central, and southern Italy; southern Spain; and southern France. Second, most of them are very distinct morphologically. Third, with respect to incompatibility (S-alleles), they fall into four distinct groups: 1) 'Tonda Romana' (S_{10} S_{20}), and 'Negret' (S_{10} $S_?$); 2) 'Barcelona', 'Montebello', and 'Riccia di Talanico' (all S_1 S_2) and 'Tonda Gentile Delle Langhe' (S_2 S_7); 3) 'Tombul' (S_{12} S_{13}); and 4) 'Tombul Ghiaghli' (S_4 S_8) (Thompson 1979). Within these groups the presence of a common allele could, but not necessarily does, indicate a relationship. However, between the four groups there could be no common genetic origin.

These eight heterozygous cultivars comprise the major portion of the world's hazelnut production. The total area planted to them probably exceeds 350,000 ha in four major producing countries. Therefore, it would be expected that nondormant segregants would occur frequently among chance seedlings, which are of common occurrence near commercial plantings. While they would not survive long in the colder regions, e.g. Oregon or northern Italy, they should survive for many years in the warmer regions near the Mediterranean and Black Seas. It is puzzling that this phenomenon has not been reported previously.

The occurrence of nondormant hazelnut trees provides an evolutionary mechanism which could, theoretically, greatly extend the range of this species. Rather than being limited to temperate regions which have sufficiently cool winters to satisfy the chilling requirements of normal trees, these mutants should thrive in subtropical regions. That the wild species has not moved southward by means of the nondormant mutants is perhaps due to the inhospitable, hot, arid climatic zone lying directly to the south of its natural range in southwest Asia.

Although climatic barriers restrict the natural spread of the species, nondormant hazelnuts might possibly be cultivated in moderate subtropical regions, such as the tropical highlands, where no chilling temperatures occur and summer temperatures are not high. In recent years there has been much interest in developing temperate fruit and nut crops adapted to the tropical highlands. Successful methods for achieving this goal include breeding for low chilling cultivars (Mowry and Sherman 1984; Scorza and Miramendy 1981; Sherman and Sharpe 1976) and using cultural methods such as defoliation (Janick 1974). Nondormant hazelnuts appear to be good candidates for trial in these regions. Hazelnuts are adapted to mild, not severely hot, summers and can tolerate high humidity, although a dry period would be necessary at harvest time to dry the nuts. Based on limited experience under greenhouse conditions, nondormant mutants appear to be unresponsive to photoperiod and may grow continuously. Nuts have high nutritional value, are less perishable than fruits, and can be handled and transported readily in the shell. Should growth and reproduction of nondormant hazelnuts prove satisfactory in the tropical highlands, a breeding effort may be warranted to develop cultivars adapted to these conditions. The presence of this mutant allele in the world's best cultivars provides an excellent germplasm base for such a program.

In the Oregon breeding program the frequent segregation of nondormant seedlings creates an undesirable and expensive nuisance. All seedlings are grown in the greenhouse for one year and then planted in the field in October before the rainy season begins. The nondormant trait is not identifiable at this time. Because all mutants are eventually killed by low temperature, the time, labor, and space allocated to growing them is lost. Thus, identification of this genotype at the seed or very young seedling stage would be very advantageous. Early identification would be an even more valuable tool when selecting for the trait rather than against it.

The discovery of nondormant mutants in *C. avellana* suggests the possibility that similar genes may exist in other temperate fruit and nut crop species, although none have been reported. If nondormant segregants did occur in a temperate tree breeding program they would likely suffer freeze damage during the first winter in the field and be lost or discarded for lack of hardiness. Geneticists and breeders of temperate tree crops should consciously search for nondormant genotypes. Such mutants could contribute to greatly expanded fruit and nut crop potential in warm climatic regions.

This single gene mutant that apparently blocks the development of all the physiological and morphological changes associated with dormancy should provide an excellent tool for studying fundamental mechanisms of dormancy induction in temperate trees. While previous studies of dormancy inheritance have indicated multiple gene action, here, clearly, is a single gene that regulates a pivotal process for the normal expression of other genes. Perhaps the mutant affects the photoperiodic receptor system in leaves which appears to be phytochrome-mediated in many plants (McKenzie et al. 1974), or a translocatable phytohormone which may transmit the message to other plant tissues.

Because dormancy mechanisms in buds and seeds may be similar, it would be convenient to use seeds from nondormant hazelnuts as experimental tools. Homozygous embryos are easy to generate by crossing heterozygotes, but dormancy is induced in hazelnut seeds by the testa and shell, both heterozygous maternal tissues, rather than by the embryo itself (Jarvis 1975). Therefore, two mutant trees must be intercrossed to obtain the desired research tools – seeds whose embryos and seed coats are both homozygous recessive. This, as yet, has not been accomplished.

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