REGENERATION OF COPPICE

by

N. Lust & M. Mohammady

The chief characteristic of coppice is its ability to regenerate by vegetative reproduction.

Vegetative reproduction is an ability possessed by many woody species and is an important means of survival.

In areas where forest fires are frequent, trees having the ability to regenerate by vegetative reproduction are the ones most able to survive.

1. Methods of Regeneration

Regeneration of coppice can come about in three ways :

1. by stump sprouts (stool shoots);
2. by root sprouts (root suckers);
3. by seedlings.

This simple classification, however, is not generally acceptable and it is the origin of certain contradictions or misunderstandings.

Poskin (1949) gives the following classification :

1) Stool shoots (stump sprouts) :
   - sprouts originating from dormant buds;
   - sprouts originating from adventitious buds.
2) Root suckers (root sprouts)

   A further distinction is made between :
   - sprouts produced by roots (usually superficial roots) and caused by mutilation of the tiunk or of the organs under the ground or by the natural or accidental dying off of parts above the ground;
   - shoots arising from root buds (birch, especially) and emerging from the ground at a distance of less than one centimeter from the trunk;
   - false sucker shoots or adventitious shoots on the roots resulting from a wound or cut on the roots.

3) Natural seedlings

Kramer and Kozlowsky (1960) on their side distinguish between :

— stump sprouts, which arise from root collars and the lower part of the tree trunk and develop from dormant buds;

— stool shoots which develop from adventitious buds and arise between the bark and wood of stumps;

— root sprouts or root suckers which arise from adventitious buds on the roots.

In the category of stump sprouts, Smith (1962) particularly distinguishes "seedling sprouts" meaning sprouts arising from stumps less than 2 inches in diameter.

In a study on sweetgum (*Liquidambar styraciflua* L.) Johnson (1964) presented the following classification :

— top sprouts : emerging from the stump having no direct connection with the soil :

— collar sprouts : a junction with the stump visible at ground level.

— root sprouts : developing within an area of 2 feet from the stump.

Poskin, Kramer and Kozlowsky as well as Smith, consider the origin of shoots a basis for classification.

Johnson, on the other hand, stresses the question as to whether or not there is a direct junction or contact between the new shoots, and whether they depend for the transport of water and minerals on an older root system from which they cannot be separated or else have not the opportunity to develop a separate root system.

1.1. *Regeneration by stool shoots*

A distinction is generally made between stool shoots arising from dormant buds and those coming from adventitious buds. Closer attention must therefore be paid to these two types of buds.

1.1.1. Dormant buds

Most buds are formed in the axils of new shoots. Some buds sprout the following year or shortly after and develop into new shoots. A considerable number, however, remain sleeping or inactive during an indefinite period. These are the dormant buds, which have the same age as the tissue from which they arise. They show the phenomen of yearly growth, because they possess the lateral and apical meristems, but they always remain under the bark. They remain in contact with the cambium. Their annual growth is comparable to that of the secondary stem, often with the formation of annual rings. The branching of dormant buds often occurs (Kormanik and Brown, 1964).

Chandler (1947) presents evidence that secondary dormant trace buds originate in the axils of bud scales. A primary dormant bud can become the ancestor of numerous secondary buds, with its trace branching and extending to them (Aaron, 1956). Dormant buds at the stem base of certain pines e.g. shortleaf pine (*Pinus echinata* Mill.) often not only keep pace with diameter-growth of the parent axils, but form laterals which branch again. This produces the effect of a tree within a tree (Kozlowski 1971).

In sweetgum dormant buds showed patterns of both multiple and dichotomous branching. In the latter case forking resulted in the abortion of the apical meristem of the dormant bud trace. This may have been due to insect or frost damage to the buds in the periderm, stimulating the release of two bud scales (Kormanik and Brown, 1964).

Questions have been raised as to whether survival of dormant buds requires their connection to the pith by a bud strand or stele. Strasburger & al. (1912) thought that, dormant buds sometimes stayed alive and continued to grow after losing their connection with the woody parts of the parent stem.

Recently, however, Kozlowski (1971) identified dormant buds by their bud trace to the pith.

If the physiological balance of a tree is disturbed dormant buds may sprout. This can happen after cutting damage, fire or disease, all of which more or less destroy the balance between absorption of nutrients and actual requirements or drastically modify light radiation conditions. In the same way, the appearance of shoots at the basic of older trees frequently indicates a physiological disturbance.

In some cases however, dormant buds completely lose their ability to sprout (Smith, 1962) :

a) when the connection is severed between the pith of the dormant bud and the pith of the original stem;

b) when the bark, covering the dormant bud, has become too thick so that it becomes impossible for the bud to break through and develop into a sprout.

The thickness of the bark as well as the possibility that the strand of the dormant bud may be severed increase with age. Thus the sprouting capacity of a tree decreases with its age.

Buds are formed every year in great number, but only a few of them sprout in the next growing season. Ward (1964) established, that about two thirds of the lateral buds formed on apical shoots of young spanish oak (*Quercus rubra* L.) remain dormant and failed to produce branches the subsequent year.

The quantity of dormant buds depends on the species. They are generally rather scarce on most conifers. According to Guinier & al. (1947) dormant buds are never found in *Pinus* sp. and rarely in the *genera Abies* and *Picea*, but more frequently in *Taxus* spp. They are on the contrary, more numerous in hardwood trees, especially oaks, hornbeam, maple, etc.

As was proven, Guinier was completely mistaken where *Pinus* spp. are concerned.

There is a clear difference between dormant buds and normal buds. Dormant buds are always small, irregular in shape, and the few scales they have consists of a corky substance. These buds can easily be seen on the twigs of oaks, beeches, etc. They can also be observed on the branches and trunks of trees as long as the bark is smooth. When the bark becomes grooved, the buds become indistinct but persist nevertheless.

Shoots sprouts from dormant buds have the greatest importance for the regeneration of coppice. They have a firm and compact base because of their close relation to the stool. They are well protected from damage by circulation-, wind-, and snow because they develop around the stool. They also develop at the junction with the soil when trees are cut close to the surface of the ground. In some cases they grow roots and can thus break away from the mother stool. Most of the time they do not leave the junction with the stool.

1.1.2. Adventitious buds

Many woody plants have the inherent potential of producing buds in parenchyma tissues not directly associated with apical meristems, and in places not dictated by their normal phyllotactic patterns. Buds arising in this manner are termed adventitious (Zimmermann and Brown, 1971).

These buds form rather irregularly on older parts of the plant. They vary as to their origin and may spring from deep-seated or peripheral tissues. Most adventitious buds in woody stems form in the cork cambium (phellogen), phloem and parenchyma, or in the initial rays of the vascular cambium. In many trees, adventitious buds arise in response to wounding followed by proliferation of callus cells of one of the above mentioned tissues.

Zimmermann and Brown (1971) do not agree with Guinier & al. (1947) who stated that adventitious buds "only" develop on the thickenings which surround the section of a trunk or of a severed branch.

Adventitious buds in undisturbed shoots are of exogenous origin. In such cases they arise in superficial tissues near the surface of the stem, such as interior cortical or phellogen cells which normally proliferate in connection with lenticel formation.

The main difference between adventitious and dormant buds is the lack in the former of a bud trace all the way to the pith. Adventitious buds usually produce a shoot without passing through a dormant period, and their activity is apparently regulated by hormonal balance (Eliason, 1961).

Shoot developing from adventitious buds is less frequent in species featuring a great number of dormant buds. In most species with few dormant buds, such as beech and birch, adventitious buds are more frequent and very valuable.

Sprouts arising from adventitious buds have not nevertheless the same value as those spruning from dormant buds. They are thinner and not sc firmly attached to the mother plant. Their location at the upper surface of the stool, exposes them even more to damage from various causes (Poskin, 1949).

The appearance of a wound on the stool can cause the formation of adventitious buds. Wounds are healed in two ways (Guinier, 1947) :

a. chemical cicatrization (passive); this consists in the drying up of cells on the surface of the wound, where several secretions, mainly tannins and resins, accumulate. In this way an impenetrable scab is formed, which protects the deeper tissues.

b. cicatrization by multiplication (active); this consists in a thickening of tissues (detrimental to living cells), which takes the properties of the missing tissues, and arises on the surface of the wound.

   A great number of adventitious buds arise on the scarred tissue (of the wounds) in stools and roots, caused by cuttings or by other accidents resulting from exploitation.

1.2. *Regeneration by root sprouts*

Root sprouts arise from adventitious buds formed on the roots. All buds on roots are adventitious in origin, and most arise exogenously from tissues exterior to the stele. There are, however, instances where they appear to arise endogenously from the pericycle as do lateral roots (Zimmermann and Brown, 1971).

The question often arises whether young meristems, giving rise to lateral roots, can alter morphogenetically so as to form buds. In studying the origin of young primordia in roots of horseradish (*Rorripa armoracia*) Dore (1955) found that most organized meristems occurred in the phellogen of the main root in close association with scars of older lateral roots. Such meristems can develop into either buds or roots, depending upon the physiological conditions prevailing at the time. At high auxin levels, the ratio of roots to buds increased, whereas at lower auxin levels, more of the apparently neutral primordia developed into buds.

Most adventitious buds form sprouts in the same season; hence they do not normally undergo dormancy. This, for example is, the case with root sucker formation in the *genera Populus*, *Robinia* and *Rhus*.

In sweetgum, however, numerous buds are initiated endogenously or exogenously, on both young or old trees. They may become dormant, but prevail for several years as suppressed buds, embedded in the periderm of the root, before being released to form root suckers (Kormanik and Brown, 1967).

In view of this observation, other woody species may also produce suppressed buds which stay alive for varying periods of time before being released to form root suckers.

Farmer (1962) studied some physiological aspects of root suckers initiation and initial growth in quaking aspen (*Populus tremuloides Michx*) and bigtooth aspen (*Populus grandidenta Michx*).

He made the following observations :

1. Suckers on quaking aspen were found on shallower, smaller parent roots than was the case on bigtooth aspen.

2. Light had no direct relation to sucker formation, but a temperature increase from 50 to 80° F shortened the time for initation and development of suckers on both species.

3. Considerable clonal variation in suckering were observed in clearcut stands. In uncut stands, suckers were found each year in clones heavily infected with Hypoxylon-cancer, but were absent in healthy clones.

4. Lateral roots, severed from parent trees in root-pruning studies, gave rise to numerous suckers, but none formed on root parts still attached to the trees.

5. Girdling stem phloem near the base of trees consistently failed to stimulate sucker formation.

6. In field experiments, full shade (100 foot-candles) reduced the occurrence and growth rate of suckers of quaking aspen but not of bigtooth aspen. Since the paiental root diameter was less

for quaking aspen than for bigtooth aspen, the specific difference in carbohydrate storing capacity may have caused the variation of growth response.

Partial shade (4.000-6.000 foot-candles) had no significant effect on height growth of either species in the first season.

7. In controlled environment experiments with quaking aspen, reduced light intensity was not associated with decreased height growth under a 65°/70° F (night/day) temperature regime, but plants grown at 500 foot-candles showed reduced height growth compared with those grown at 1.700 footcandles at a temperature of 72°/76° F.

A chlorosis-like discoloration was characteristic of aspen leaves growing in artificial light.

Research has been carried out by Börset (1956) and Smirnov (1959) regarding the density of root suckers. Börset (1956) studied two stands, at intervals of 2 and 5 years after clear-cutting. On one plot he counted an average of 8, 2 residual stumps per dekare with 1.800 suckers, on the other plot he found 47 stumps with 7.000 shoots per dekare.

The most densely stocked plots carried a number of suckers corresponding to 22.000/dekare. He found a slight but significant correlation between the number of suckers on a plot and its distance from the nearest stump or the nearest five stups. Most of the suckers sprang from thin roots, having a diameter of 0.5 to 2 cm.

Most of the suckers sprouted from superficial roots at a depth of less than 4 cm. During the first years the suckers grew to a fairly good height though they were often damaged by fungi, mainly *Venturia tremulaea*.

The average height of the suckers was 81 cm after 2 years. The plot showed slight positive correlation of height with root diameter and root depth.

Smirnov (1959) found in the upland of the Tellerman forest, that given favourable conditions, in the upper 20 cm of the soil roots produced a large number of suckers, namely up to 200.000 per ha after clear felling of a mature stand, and up to 73.000 per ha after an intensive cleaning in a young stand.

The following conditions have a favourable influence on the formation of aspen suckers :

— good soil aeration and shallow location of the roots;

— thin root bark and small root diameter;

— sufficient soil moisture;

— sufficient warmth.

To increase sucker production in black locust (*Robinia pseudoacacia* L.) Ceremsky (1969), deliberatly caused wounds on the roots.

According to Guinier & al. (1947) pine trees do not have the ability from one species to the other. Spanish oak and hornbeam fail to produce root suckers, while evergreen holly oak (*Quercus ilex* L.) and cork oak (*Quercus suber* L.), elm, aspen and robinia in particular produce numerous root shoots.

According to Kramer and Kozlowsky (1960), Smith (1962) and Kozlowsky (1971) formation of root suckers is rare in American tree species except in black locust and several types of poplar. Smith (1962) also mentions the appearance of root suckers on American beech (*Fagus grandifolia* Ehrh.) but these shoots are very susceptible to rot. Poskin (1949) points out the formation of root shoots in white alder (*Alnus rhombifolia* Nutt.) and Tschermak (1950) in *Ailanthus glandulosa* Desf. Eggeling (1949) states, that sucker production is more common in savanna forests than is generally realised, especially in grazing areas where the trampling of the surface roots provides the necessary stimulus for sucker production.

Root suckers are less susceptible to buttrot than stump sprouts. Furthermore, they are not confined to the old stump, but may spring up over wide areas around the parent trees. As a result, stands arising from root suckers are stocked much more evenly than those consisting of scattered clusters of stump sprouts (Smith, 1962).

1.3. *Regeneration by seedlings*

In principle coppice does not regenerate by seed. Natural seedlings, however, appear regularly in coppice and are often very valuable. They come from seeds of nearly trees. At first they are left to grow among the coppice. In due time, they are cut during the subsequent exploitation, so that they become stools.

When natural seedlings do not appear in sufficient number in unoccupied parts of the forest, they can be provided foı by seedling or planting. Artificial seedlings (like natural seedlings) have the disadvantage that they grow more slowly than stool or root shoots during the juvenile stages and risk to be suppressed or die off.

Cut back transplants of some species (ash, maple) can be used to fill up the gaps if planted before the beginning of the growing season. Such plants can form powerful shoots, which have a better change of surviving than original stool shoots.

When the rotation period is long enough (e.g. 40 years and more) the mother stand is normally able to produce sufficient seed and natural reproduction can be relied upon to furnish a mixture of seedlings with sprouts, especially if the stand is well thinned.

Regeneration by seedlings is often necessary in the coppice selection system. Young shoots have to be preserved for the future, so the cutting must be done at a certain height above the ground. This results in new shoots appearing too high to form their own independent root system, consequently the stool dies sooner or later and has to be replaced by a new stand.

2. Factors Affecting Sprouting

Several factors influence the formation of new shoots, among them the physiological characteristics of the species, the cutting season, the cutting method, age and reproduction capacity of the stool, the site.

2.1. *Species*

It is well known, that deciduous trees form more shoots and form them much more easily than conifers, but the variability from one species to another is considerable in each group.

Even within each species great variation occur. The oaks of the mediterranean regions, such as Quercus ilex and Quercus suber, form both stool and root shoots, while the more northern oaks like Quercus robur and Quercus petraea do not develop root shoots. Little (1938) observes that white oak (*Quercus alba* L.) and post oak (*Quercus stellata* Wangenh.) had more, but shorter sprouts per stump than did black oak (*Quercus velutina* Lam.) and scarlet (*Quercus coccinea* Muenchh.).

2.2. *Cutting season*

It is generally admitted that the best results are obtained when the cutting takes place during the dormant season and the worst when cutting is done after the appearance of the leaves. The presence of sap in the wood at cutting time increases the liability of the stumps and sprouts being injuried such as by tearing of bark, breaking off of sprouts and damage from forst (Hawley, 1949).

It has generally been held, that sprouting vigour is closely related to the availability of carbohydrate reserves so that a seasonal sprouting vigour is to be taken into account with a minimum occurring in early summer (Aldous, 1929).

Clark and Liming (1953) found that practically all sprouting of oak takes place during the first and second growing season after girdling. Sprouting is delayed to the second year for trees girdled late in the season. Many stumps will sprout for a number of years after cutting if the sprouts from the previous year have been removed, but they usually sprout best during the first year after cutting. These observations suggest, that the sprouting vigour decreases if carbohydrate reserves are low or nearly exhausted.

Wenger (1953) found nevertheless, that the formation of shoots in sweetgum in South Carolina was independent of the carbohydrate content. He suggested that a hormone system, related to that controlling apical dominance, governs sprouting vigour.

Kramer and Kozlowsky (1960) conclude that at the present time, physiological control of sprouting is not satisfactorily explained. This problem deserves more attention and further study.

1.2.3. Cutting methods

Regeneration of coppice depends mainly on the method of cutting.

Poskin (1949) and Cochet (1963) premise the following rules :

1. Avoid rupture of the bark and bursting of the stool.
2. The cut surface must be smooth and so shaped that all the water can run off.
3. The cut must be as close as possible to the soil.

Indeed, it is very important that after cutting, some of the shoots develop their own root system, thus creating new young independent stools. In this way the persistancy of coppice is assured. A cut close to the soil normally gives the best results for the formation of root shoots.

On sites exposed to floods, the cut must be made higher for the cutting surface may not be located unter the water surface.

In the past the use of a saw was advised against because of the following reasons :

1. appearance of a spongy cut-surface which holds up the water;
2. danger of tearing the bark.

However Poskin does admit, that judicious usage of a saw can have positive results as well.

Recently motor saws have been hused more frequently. Cochet (1963) confirmed, that the use of mechanical saws had no adverse influence on the coppicing power.

2.4. *Age and size of stump*

According to Hawley (1949) the sprouting ability of trees decreases, as they become older and larger. Although the real cause is unknown, the author thought it might have some relation to the ability of the seed formation of that species.

When the trees start to produce seed, the dormant bud would lose their power to sprout and adventitious buds would stop forming.

Kramer and Kozlowsky (1960) claimed, that the number of sprouts per stump increases with the diameter until the increasing thickness of the bark begins to hinder the emergence of dormant buds. The possibility of bud traces being interrupted also increases with time.

The increase in the number of sprouts with increasing age and size occurs because a longer time permits more extensive branching of the original bud traces. It is also possible, that the dormant buds at the base of the tree, are less inhibited by active buds in the tree top when trees grow larger.

Wenger (1953) suggested, that sprout size may be related to the effects of the size of the root system on the water and mineral nutrients supply, as well as to availability of mineral nutrients. Poskin (1949) attaches much importance to the state of health of the stools. A healthy root system would be the first condition to form root shoots.

The age at which trees are still able to form shoots, differs considerably from one species to another.

Hawley (1949) stated that the thriftier the tree and the nearer it was to its maximum growth rate when cut, the better the stump sprouted. This period of greatest thrift and highest growth rate extends over the first part of tree-life and may be considered as passed after the thirthieth year.

2.5. *Site*

Sprouting is usually more vigorous on good sites than on poor ones. The improved growth on better sites probably resulted from a greater availability of moisture and minerals and perhaps from a larger food supply in the stumps.

Poskin (1949) also stressed the influence of climate on shoot formation. Coppice needs a mild climate, with a long vegetation period, otherwise shoots suffer too much from frost. Light and warmth highly stimulate the formation of new shoots. Sprouting ability is better in strong light than in the shade, better by exposure to the south than to the north, better in the plain than on hill and mountain slopes, and better in southern than in northern countries. As a general rule late frost is most harmful.

Questions are sometimes raised as to the ability of sprouting species to reproduce vigorously after repeated generations of sprouting (Hawley 1949).

Two important points appear to be involved here : the effect of decay spreading from old stumps and thus attacking the generation of sprouts, and second, the gradual deterioration of the site and lowering of production, due to frequent exposure and extensive use of mineral nutrients by the coppice crops.

It is believed that little loss in vigour of sprouting occurs as a result of the entrance of decay. What does happen is that with susceptible species decay may advance so rapidly from the old stump to the new sprout, as to prevent (except on very short rotations) the production of crops free from early and serious infection.

European opinions incline toward the belief that continued cropping on coppice rotations reduces production. A lowered production may not be experienced on the moister soils, to which the coppice method is best adapted, and with provide a larger supply of available nutrients than poor, dry sites.

3. Sprouting of conifers

Little is known about the sprouting capacity of conifers. In most European handbooks it is even stated that conifers do not possess the ability to sprout. Several coniferous species, however, are known to sprout, especially after fire. Among the conifers which have good sprouting ability are redwood (*Sequoia sempervirens* Endl.), pitch pine (*Pinus rigida* Mill.), short-leaf pine (*Pinus echinata* Mill.), pond pine (*Pinus serotina* Michx.) and bald cypress (*Taxodium distichum* (L) Rich.). (Kramer and Kozlowsky, 1960.)

Cheyney (1942) states that only three american conifers, short-leaf pine, cypress and redwood, produce sprouts that will grow to marketable size.

Although redwood is considered a good sprout producer, Person and Hollin (1942) found that sprouts provided less than 10% of the full stocking. The stumps of old-growth stands are so widely spaced, that sprouts are only sufficient to restock a small fraction of cutover areas. The spacing of trees in an second-growth stand may, however, be close enough to allow the use of the coppice method. Techniques remain to be developed and tested.

According to Smith (1962), redwood is the only american conifer, that can satisfactorily be reproduced from sprouts. Redwood sprouts are straight and highly resistant to decay and make a durable contribution to regeneration after any kind of cutting.

Neal (1967) arrived at the following conclusions about sprouting of old-growth stumps of redwood :

1. The probability of a stump sprouting varied inversely with its diameter.

2. The number of sprouts per sprouting stump and the height of the tallest sprout were not related to the stump diameter.

3. The lower portions of stumps sprouted more and produced more sprouts than higher parts.

4. The height of the tallest sprout varied according to the number of sprouts.

5. Different kinds of damage produced varying sprouting responses.

In short-leaf pine (*Pinus echinata* Mill.), the occurrence of sprouting is well known. At first Mattoon (1908) thought such shoots to be adventitious and arising from the upper portion of the root and the lower stem part.

The origin of these shoots was accurately determined by Stone and Stone (1954). Young seedlings of short-leaf pine normally have a double crook near the base of the stem. The lower, most primary, needles almost invariably bear axillary buds and numerous buds are found above this zone as well.

The lower buds often show a cluster just above the cotyledones. Rootlets from the uppermost root tissue arise in close proximity to the bud cluster, which is often buried by soil movement or litter accumulation. Thus it is not strange, that these buds and the subsequent shoots have been thought to arise from root tissue. Sectioning, however, always demonstrates that they originate in the stem (Stone and Stone, 1954).

Some buds may develop into shoots during the first few years, but seldom attain appreciable size as long as the parent stem is growing normally. The remaining buds persist in a more or less dormant condition, sometimes giving rise to small clusters of fascicled needles. These clusters, as well as the apparently inactive buds, may branch several times, considerably multiplying the original number of buds. Injury to the stem, due to fire, grazing or cutting, provides a stimulus for elongation of these buds and often leads to abundant sprout production.

Although basal sprouts are usually associated with young trees, Little and Somes (1956) found basal sprouts on short-leaf pine trees up to 30 years old. But they suggested that the capacity of short-leaf pine to produce basal sprouts depended more on tree vigour, basal crook, and on root-collar diameter rather than on the age of the tree.

TABLE 1

Sprouting condition of burned trees at the end of the growing season (Phares and Crosby, 1962)

condition of main stem	condition of sprouts	trees		average height of tree before burn (feet)
		Number	Percent	
alive	no sprouts	10	4.3	4.8
alive	alive	31	13.4	4.6
alive	dead	0	0	—
top killed	no sprouts	17	7.3	2.2
top killed	alive	147	63.4	3.3
top killed	dead	27	11.6	4.8
	Total	232	100	—

Phares and Crosby (1962) made a study of the relation between sprout occurrence and growth and the size of young short-leaf pine trees injured by fire. In the spring of 1956, they planted 1 year old seedlings. In April 1959, the area was control-burned. At the end of 1959, they examined each tree for mortality, number of basal sprouts and height of the tallest sprout on each tree.

1. Basal sprouts had developed on practically all top-killed trees
2. Most non-top-killed trees were weakened enough to let some basal sprouting occur. This is an interesting finding as common belief is that top-kill is necessary to stimulate basal sprouting.

Phares and Crosby (1962) found more basal sprouts per tree on the taller than on the shorter ones, undoubtedly because the larger trees had a greater basal diameter and more basal buds.

Moreover the tallest sprouts were found on the largest trees, probably because these trees had larger root systems, that were better able to supply the moisture and mineral nutrients. The height of the tallest sprout, however, did not appear to be affected by the number of sprouts on each tree.

It has commonly been believed, that loblolly pine (*Pinus taeda* L.) sprouts little, if at all. For example Grano (1956) stated, that young short-leaf pines sprouted after being severely damaged, while lobloly pines did not.

Little (1953) said, that sprouting in the latter species was negligible. However, rabbits clip thousands of loblolly pine seedlings, and as Wakely (1954) noticed, many of these recover.

Little and Somes (1950) examined under what conditions and until what age loblolly pine may sprout.

Pinus teada seedlings may produce sprouts from two sources. One is from buds at the nodes (the point on the stem at which normal lateral buds occur or have occured), the other from dwarf shoots or the sites of dwarf soots. Of these two possible sources, the latter is by far the more important. The proportion of axils that develop needle fascicles, as well as the height at which the first fascicles are formed, varies with growing conditions. Most loblolly pine seedlings growing under relatively unfavourable conditions in the wild, develop only primary needles on the lower 6 inches of their stems or, at most, only a few fascicles. In contrast, nursery seedlings may develop numerous needle fascicles in the axils of primary needles, starting as low as 2 inches above the cotyledons.

For either loblolly or other pine species to sprout and recover after death of the stem it is absolutely necessary that a sector of the stem cotyledons remains alive. Indeed, sprouts can only develop from dormant buds, budbearing fascicles or dwarf shoots, or possibly from meristematic bud primordia, all of which originate either in a primary needle axil or at a node. Pines seem incapable of generating stem primordia from tissues of the hypocotyl or of the roots.

The ability of loblolly pine to produce sprouts decreases rapidly with age. Little and Somes (1960), observed that seedlings more than 8 years old did not even start to sprout after the severance of stems about 0,4 foot above ground, while nearly all seedlings 1 or 2 years old sprouted after similar cutting. In the youngest seedlings, no buds were visible before clipping, but later inspection indicated that either minute buds or meristematic buds primordia were probably present but lay hidden within the bark. Not all seedlings that sprout survive, and mortality seems to increase with age.

Loblolly pines do not sprout after fire because all the buds are situated above ground and thus are easily killed. Loblolly pines differ from pitch and short-leaf pines in this matter (Little and Somers, 1960) :

1. It does not normally develop a basal crook, which in the latter two species protects dormant basal buds by bringing them in contact with the ground.
2. It does not have dormant buds protected by thick bark along the bole.

Illick and Aughanbaugh (1930) wrongly described the sprouts of pitch pine (*P. rigida* Mill.) as originating from adventitious buds at the root collar, where the stem and the root system of the young tree meet. ("Root collar" or "collar" designates the juncture of hypocotyl and primary root in seedlings. By extension it also comprises the zone of contact between the root and the stem in larger trees). Stone and Stone (1954) succeeded in proving, that the origin and behaviour of pitch pine basal buds do not show an essential difference from those of short-leaf pine. A well-marked basal whorl is common, although perhaps less pronounced than in short-leaf pine. There is a greater tendency for development of strong lateral branches from the basal buds even in the absence of injury.

Many of the lower primary needles of longleaf pine (*Pinus palustris* Mill.), especially the lowermost, give rise to axillary buds (Stone and Stone, 1954). Under favourable growing conditions a number of these buds elongate slightly and produce one or more fascicles laterally, thus becoming almost sessile branches. Strong stimuli such as mutilation, heavy fall fertilization or, occasionally infection with Cronartium induce the formation of both primary and fascicled needles from such buds.

Such buds are important for the survival of injured seedlings, but they seldom persist after an increase in height has begun. Only occasionally will saplings as large as 2 to 4 inches d.b.h. be found with needle clusters near the ground.

Garin (1958) mentions an experiment with longleaf pine, planted in deep loamy sand in Central Alabama. When, 4 years after planting they begun to grow in height, the plants were axed at ground level in January. In July some of the stumps were found to be sprouting vigorously. The trees that sprouted had been severed above the root collar. Every stump observed, that had the entire root collar or part of it left, had sprouted.

Before they were cut, some had reached heights of more than 6 feet and attained stem diameters of more than one inch. In many cases more than ten sprouts were produced.

In their examination of the sprouting ability of pond pine (*Pinus serotina* Mickx.), Stone and Stone (1954) found a certain resemblance to pitch pine. A bend near the cotyledonary level is common. Usually some scattered buds can be found along the lower stem and a basal whorl is often, but not always present. The number of buds increases and the appearance of a whorled arrangement augments, when the original buds are flanked by branch buds.

Besides the rather important conifer species, mentioned above (redwood, short-leaf pine, loblolly pine, pitch pine, long-leaf pine and pond pine), sprouting was also observed in other species : in chir pine (*Pinus roxburghii* sarg.) by Troup (1916), in *Pinus* *chihuahuana* Engel., *Pinus leiophylla* Schel. & Cham. and *Pinus Teocote* Schl. and Cham. (Martinez, 1945), in *Pinus ponderosa* Laws. (Cooperrider, 1938), in table-mountain pine (*Pinus pungens* Lamb.), virginia pine (*Pinus virginiana* Mill.) (Stone and Stone, 1954), chihuahua pine (*Pinus leiophylla* var. chihuahuana (Engel) Shaw. (Shaw. 1914; Sudworth, 1917), in *Pinus gerardiana* Wall. and *Cedrus deodora* Loud. (S.A. Unaslyva, 1957).

At new Forest, Dehra Dun, a 20 year old stand of Araucaria was thinned. Every stump produced 7 to 16 coppice shoots, which were thinned to 2 per stump and after 10 years were 25 ft high and 3, 1 inch in d.b.h. (Dabral, 1961).

Furthermore sprouting is also mentioned for spruce, Scotch pine and Siberian Larch.

Nekrasova (1955) in a study about the natural regeneration of spruce in the Kola Peninsula concluded, that vegetative reproduction occurred very frequently, chiefly by natural layering. But rooting along the branches of fallen trees was widespread, and in some such cases the "young" trees coned as early as 1 year after the death of the parent tree. It is also common for seedlings procumbent in the grass, to lose their terminal bud and to develop up to 5 stems from dormant buds, each stem producing "adventitious" roots. The question arises, however, whether Nekrasova is not mistaken about "adventitious" roots.

Godnev (1950) mentions, that young Scotch pine coppice after accidental or deliberate damage to the leading shoot or main stem. Siberian Larch can be cut back to the stump and will coppice at least up to 7 years of age and probably even later (Dementjev, 1952). This treatment is beneficial to weak seedlings and should be carried out as early in the season as possible, in any case no later than the end of June. Plants more than 2 years old are liable to form several coppice shoots, of which all but one should be removed. This treatment appears to accelerate growth in height.

Seedling sprouts often develop into well formed trees and many acceptable stands of pitch, short-leaf and long-leaf pine are known to have originated in this manner (Stone and Stone, 1954). On the other hand, Godnev (1950) points out, that it is possible to cut back abnormal nursery plants as well as damaged ones, and to use them later on to fill in empty places. These cut-back plants fill up the areas very quickly because of their strong growth.

4. Decay in sprout stumps

The formation of sprouts after cutting cannot strictly speaking be considered as a true regeneration phenomen, but rather as a method of regeneration, as it is evident that new sprouts always develop on the same stools.

The stools are weakened by periodic felling, their ability to sprout slowly decreases and is eventually lost. According to Poskin (1949), two facts can prolong the life of coppice :

1. formation of wound tissue by cicatrization, which prevents stool rot;
2. the appearance of natural seedlings, which can replace the dead stools.

Decay in the old stumps may in due course infect the buds of the new sprouts. The progress of such decay varies greatly with the species of tree (Hawley, 1949). Some species are affected very slowly and to a small extent, while others decay rapidly and are exceedingly injuried. Oak and hornbeam can continue forming new stools for a practically indefinite periode, no matter how many cuttings they undergo. They seem to suffer very little from partial stool rot. Other species, like ash, birch and most other softwood species, keep their ability of sprouting for 2 or 3 rotations only (Poskin, 1949).

Roth and Sleet (1939), in studying 7 species of oak found that considerable butt rot occurred in sprouting oaks stands. Decay in the sprouts came from the old stumps and entered the sprouts only after heartwood had begun to form, making a connection with the heart of the stump. The height above ground at which sprouts originated on the stump was an important factor in determining the presence of decay. Only 10% of the sprouts originating below ground level showed decay, at ground level only 20%, but at 4 inches and more above the ground more than 40% of the sprouts were affected by decay.

Extensive studies of decay in sprout oak stands established (Roth and Sleeth, 1939; Roth and Hepting, 1943) that in trees originating from sprouts the tendency to decay was definitely related to the height of the sprout originating on a stump, the size of the parent stump and the size of the wound created by the eventual decay of the parent stump. Of these factors, the height of the sprout origin was particularly important. Almost no decay from the rotting parent stump developed in sprouts rising slightly above ground level, whereas half or more of the sprouts had started to rot if they rose three or more inches above the ground.

Cutting the stumps down close to the ground and thereby forcing the sprouts to originate less than 4 inches from the ground is evidently an important point in the coppice management of oak.

The longer the rotation period, the more danger there is of decay seriously infecting the sprouts. because the evil has more time in which to spread and because sprouts on large stumps are more rapidly infected than those on small stumps (Hawley, 1949). The ideal condition, from the point of view of resistance to decay, is to have the new sprout completely take over the root system of the old stump. Then the entire root system remains alive, the top of the old stump becomes completely callused-over, and thus decay is less likely to attack the sprout.

Heffelman and Hawley (1925) have shown, that for oaks in southern New England this ideal condition is attained only with stumps averaging 2 inches and less.

A study spread over more than 30 years has been made by Roth and Hepting (1969) with the following aim:

1. to evaluate the earlier estimates of expected butt cull in a new sprout stand, based on the heights of origin of the new sprout trees;
2. to determine if most of the butt cull could be prevented when only sprouts of low origin were permitted to form the final stand.

A certain number of plots were laid out in a 50 to 60 year old mixed oak sprout stand on the George Washington National Forest Virginia. In all cases 12 inch high stumps were left (Table 2).

TABLE 2

Number of 12 inch high stumps sprouting, and percentage of trees decayed, by species, for those arising at or below ground level, and those arising one inch or more above the ground (Roth and Hepting, 1969)

Species	Sprout origin at ground level or below			Sprout origin 1 inch or more above ground		
	Sound sprouts	Decayed sprouts		Sound sprouts	Decayed sprouts	
	No.	No.	%	No.	No.	%
White oak	126	37	21	52	32	38
Black oak	50	7	12	61	29	32
Scarlet oak	68	7	9	20	16	44
Chestnut oak	18	1	5	7	0	0
Red oak	—	—	—	0	2	100
All species	262	49	16	140	79	36

1. Although the stools were 12 inch high, 59% of the sprouts appeared at the ground level or below.

2. In the shoots appearing at ground level or below, 16% of the sprouts were decayed, while 36% of the shoots appearing higher were affected.
3. Essential differences existed between the various species. For white oak (*Quercus alba*) 21% of the sprouts, appeared at ground level or below, already decayed, while only 9% in scarlet oak.

When the sprouts were five years old (in 1940), it was estimated that 32% of the trees could be expected to be butt rotted at 40. This was based on the heights of origin of the dominant sprouts at 5 years of age (Roth and Hepting, 1943). When the trees were cut after 32 instead of 40 years, the actual percentage of decayed trees was 24%. Had these plots been permitted to stand 8 additional years, there would unquestionably have been a higher percentage of decayed trees, because the heartwood would have more frequently been united with the decaying parent stumps.

Roth and Hepting (1969) also laid out experimental plots, where cutting was carried out as close to ground level as possible. Only 6% of the 149 sprouts from low cut stumps were butt rotted after 32 years, compared with 24% of the 530 sprouts from high cut stumps.

Finally, to determine whether burning would kill the buds above the ground line, and thus bring about stands of low origin sprouts, 75 stumps were marked for observation in a stand of 40 year old oaks, and cut after the stand was burned in April 1934 (Table 3).

TABLE 3

The height of origin of sprouts originating from stumps in a burned-over area in 1934 (Roth and Hepting 1969)

Species	Stumps bearing living sprouts in 1967	Stumps with no surviving sprouts in 1967	Sprouts origin at ground level or below		
			Sound	Decayed	
	No.	No.	No.	No.	%
White oak	20	6	34	2	6
Scarlet oak	38	9	54	2	4
Chestnut oak	2	0	4	0	0
All species	60	15	92	4	4

1. Eighty percent of the stumps bore living sprouts in 1967 (after 32 years)
2. Only 4% of the sprouts were butt-rotted in 1967.
3. All the sprouts in the burned area included in this study, had arisen at or below the ground line.

The results of the study by Roth and Hempting (1969) clearly implied, that any measures taken at or shortly after stand establishment, which would assure sprouts of "low origin" on the parent stumps, would assure an infrequency of decay in the newly regenerated stand.

Such measures included :

a. burning over a stand after felling in order to kill buds above ground level;
b. felling at ground line;
c. felling at a time of the year, which might favour sprout formation from the buds at or below ground level;
d. cutting the high origin sprouts a few years after stand establishment so that a stand of low origin sprouts was assured.

This study also showed, that the season of cutting had no effect on decay incidence, but butt rotted parent trees tended to produce sprouts that became rotted. Most of the rot was caused by *Stereum gausapatum* Fr.

Domanski (1955) describes investigations carried out on a 51 year alder coppice stand. Of 137 coppice shoots examined, only 17 appeared to be healthy. Infection in most cases seemed to have entered from the parent stump or from dead adventitious roots. The cases of decay were related to amount of root showing above ground. Four fungus species were responsible for 77% of butt rot cases, viz. *Polyporus radiatus* (56%), *Stereum frustulosum*, *Stereum rugosum* and an unidentified fungus. In 22 cases, 2 or 3 species of decay fungus were identified in the same shoot.

In *Eucalyptus saligna at Ulbarara*, Osmaton (1954) noticed, that the replacement requirement of stools coppiced in the dry season was about 60% against 6% in the wet. The difference is probably primarily due to drought; termite damage both here and among newly planted field plants being considered secondary.

In a pine hardwood stand in Texas, Ferguson (1957) organised prescribed fires to control undesirable hardwoods. The occuring tree species were sweetgum, post oak (*Quercus stellata* var. *stellata* Wangenh.), red oak (*Quercus falcata* var. *falcata* Mickx), loblolly pine (*Pinus taeda* L.), and short-leaf pine (*Pinus echinata* Mill.).

Headfires and backfires were let on different dates, nl. May 8th, August 28th, December 17th and March 6th.

The ideal type of burning for hardwood control (one that kills a high percentage of hardwood while damaging few pines) did not seem to exist, where trees of both groups are of equal size. In general the fires that caused high mortality and damage in hardwoods also killed most pines.

Seasonal differences in the effect of the fire on hardwoods were small. Maximum effect was achieved by August burns, but fires in March and May, earlier in the growing season, also produced fairly satisfactory results. Thus there is a long growing season during which burnings may be scheduled. This is fortunate since it permits the forest manager to take full advantage of the relatively infrequent good burning days (neither too wet, nor too dry).

Dormant season burns should not be written off completely. The midwinter fires did result in substantial stem kill, and nearly as many trees were completely killed as by fires during the summer. Hazardous fuel conditions or other practical considerations may sometimes make mid winter burns preferable. The best results were achieved by headfires during the growing season. Stem kill for these fires averaged 64% for oak and 78% for gum, while respectively 14% and 23% were completely eradicated. It seems clear, that a follow up fire would have dealt with the sprouts, the largest of which were not over 40 inches in height at the end of the second growing season.

5. Conclusion

The existence of coppice is principally attributed to the different kinds of trees having the capacity to throw out shoots after being cut back. The study of the conditions and possibilities of forming shoots is extremely important.

Coppice consists of stump sprouts and suckers. In hardwood sprouts take birth both from dormant and adventitious buds. As to conifers all the sprouts seem to come from dormant buds (though until the beginning of this century, it was thought they came principally from adventitious buds). Suckers only come from adventitious buds and are only found in hardwoods.

It is not always possible to distinguish between which sprouts come from dormant and which from adventitious buds, especially as stump sprouts can also grow underground. It is characteristic of dormant buds to have a trace all the way to the pith, and this is the main difference, as there is no trace in the adventitious buds. Sectioning is a good way of discovering the origin of a bud.

The appearance of suckers is known in a few varieties of trees. They are very important because they can easily form a new, independent root system. This fact, as well as their close association with the stumps, mean that the sprouts originating from dormant buds are more useful than those coming from adventitious buds.

The origin of the shoot is very important when dealing with coppice, because the best sprouts have to be protected.

The ability to throw out shoots is dependent on several factors : the species, the season at which cutting is performed, the way in which it is done, the site, age and dimensions of the shoot.

It is not clear as to whether sprouting vigour is in any case dependent on the reserves of carbohydrates. The physiological control of sprouting has not yet been satisfactorily explained. It is generally accepted that the best results are obtained when cutting is done during the dormant period and the worst when it is done just after the trees have come into leaf.

Formerly the use of the saw was not advised, but shoot formation does not seem to be impeded by the use of motor saw.

For many kinds, though not for all, cutting must be done as near the ground as possible. This way of cutting not only stimulates the throwing out of shoots, but also fosters the formation of a strong root system, and for many species the danger of rot is lessened.

The sprouting of conifers is more theoretical than practical, except as regards a few kinds. Sproutings capacity diminishes with age and is unusual after the age of 10.

It is clear that there is a great deal of research to be done in regard to the regeneration of coppice. The following points are to be noted :

1. Research must be done according to species : not all oaks, nor all pines react in the same way. Some oaks have both stump and root sprouts, whereas others have only stump sprouts. In certain kinds of pine the dormant buds appear above ground while in other they appear below. Cultivation by controlled burning has therefore a completely different effect in each case.

2. Under what conditions are a great number of buds formed the first year? First year buds are of the greatest importance, because it is from them that the best shoots come. Have nursery saplings more dormant buds than natural ones? Should they grow under canopy (growth is delayed) or should they grow in full light? Is rich or well manured soil favourable or unfavourable? Is the branching of buds a good thing, and if so, how can it be stimulated?

3. Is the appearance of suckers limited to a few species? Is there no way of stimulating the formation of suckers, e.g. by wounding the root? Is the growth of suckers limited to the smallest roots and those nearest the surface? Do all suckers come from dormant buds?

4. How is repeated sprouting to be explained? Do the new shoots come from already existing buds or old stumps, or do they come from buds appearing on the shoots since the previous cutting? What is the latter's capacity for forming new buds. Is the relation between sprouts coming from dormant and adventitious buds stationary, or does it evolve? How long does sprouting capacity last when the rotation period is very short, e.g. as is generally the case with dieback?

5. In which kind of conifers does sprouting ability exist? Under what conditions can it be stimulated? Is repeated sprouting possible? Can root sprouts form useful elements for the future? At what height do buds appear above or under ground? Are they all dormant buds? Is root formation to be excluded? To what extent are conifer sprouts resistent to fire?

SUMMARY

The most important problems regarding the regeneration of coppice are treated here.

1. The different means of regeneration
   a) by stump sprouts
   b) by suckers
   c) by seedlings
2. The factors which determine the formation of sprouts are: the species, the season of cutting, age and dimension of stumps and the site.
3. Conifer sprouts
   A study of the way and the conditions under which the different kinds of conifers are able to sprout.
4. Stump decay.
   A study of the causes of stump decay and the way to prevent it.

Finally several subjects for research are suggested in connection with the regeneration of coppice.

RESUME

Régénération du taillis

Les problèmes les plus importants au sujet de la régénération du taillis sont traités :

1. Les différents modes de régénération
   a) par rejets de souches
   b) par rejets de racines
   c) par semis
2. Les facteurs qui déterminent la formation des coupes : l'essence, la saison des coupes, l'âge et la dimension des souches et la station.
3. Le rejet des conifères.
   On examine de quelle manière et dans quelles conditions des essences définies de résineux sont en état de pousser des rejets.

4. Le dépérissement de la souche.
On examine les causes du dépérissement de la souche, ainsi que les mesures pour enrayer ce dépérissement.

Finalement plusieurs sujets de recherche à propos de la régénération du taillis sont aussi présentés.

ZUSAMMENFASSUNG

Die Verjungung des Niederwaldes

Die wichtigsten Fragen in betreff der Verjüngung des Niederwaldes werden diskutiert.

1. Die verschiedenen Verjüngungsmethoden :
   a. Stockausschlag
   b. Wurzelausschlag
   c. Anflug
2. Die Faktoren die die Ausschlagsfähigkeit bestimmen : der Baumart, die Hiebszeit, die Schlagtechnik, das Alter und die Grösse des Stockes und der Standort.
3. Die Ausschlagsfähigkeit von Nadelhölzern.
Die Frage der Art und der Umstände des Stockausschlages von Nadelhölzern wird diskutiert.
4. Der Ferfall des Stockes.
Die Ursache des Stockferfalls, wie auch die Pflegemassnahmen zum hemmen dieses Ferfalls werden untersucht.

Zum Schluss werden mehrere Untersuchungsobjekte betriffs der Verjüngung des Niederwaldes suggeriert.

SAMENVATTING

De Verjonging van het hakhout

De belangrijkste problemen betreffende de verjonging van het hakhout worden besproken :

1. De verschillende wijze van verjonging :
   a. door stoofloten (preventieve of adventieve knoppen);
   b. door wortelloten;
   c. door zaailingen;
2. De faktoren die de lootvorming bepalen : de boomsoort, het seizoen van kappen, de wijze van kappen, de leeftijd en grootte van de stoof en de standplaats.
3. De opslag van coniferen.
Er wordt onderzocht op welke wijze en onder welke omstandigheden bepaalde naaldboomsoorten in staat zijn om opslag te vormen.
4. Het verval van de stoof
De oorzaken van het verval van de stoof, alsook de maatregelen om dit verval tegen te gaan worden onderzocht.

Tenslotte worden nog verschillende onderzoeksobjekten betreffende de verjonging van het hakhout naar voren gebracht.

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